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JOURNAL
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# THE GENERA OF BERBERIDACEAE, LARDIZABALACEAE, AND MENISPERMACEAE IN THE SOUTHEASTERN UNITED STATES[1]

WALLACE R. ERNST

BERBERIDACEAE A. L. de Jussieu, Gen. Pl. 286. 1789, "Berberides," nom. cons.

(BARBERRY FAMILY)

Perennial, rhizomatous herbs or shrubs [to small trees], often with perulate vegetative buds; plants glabrous or hairs unicellular [or uniseriate, sometimes glandular], occasionally glaucous. Leaves mostly petiolate, exstipulate (or substipulate), cauline and alternate (in *Berberis* some reduced to spines, the others fasciculate), or ± opposite (*Podophyllum*), or radical (*Jeffersonia*), simple or variously divided, pinnately or ternately compound, palmately (or pinnately) veined; stomata ranunculaceous. Inflorescences 1 to many flowered, terminal or axillary, usually bracteate, scapiform, racemose, cymose, umbelliform (or paniculiform). Flowers regular, hypogynous, often calyculate, bisexual. Perianth usually 3(–5)-merous, aposepalous and apopetalous, usually multiseriate (some-

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium, made possible through the support of the National Science Foundation and George R. Cooley, and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the style established in the first paper of the series, Jour. Arnold Arb. **39**: 296–346. 1958 (and continued through volume 44). The area covered, as in earlier treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area with supplementary information in brackets. References not seen by the author are marked with an asterisk.

Helpful information or assistance of various kinds was given by H. E. Ahles, G. K. Brizicky, G. R. Cooley, W. H. Duncan, Shiu-ying Hu, Jean H. Langenheim, R. Ornduff, Lily M. Perry, D. G. Rhodes, Bernice G. Schubert, and Lazella Schwarten. Mrs. Gordon W. Dillon prepared the final typescript. The illustrations, the continuing work of Dorothy H. Marsh, were drawn from fresh or preserved materials from Nashville, Tennessee, made available through the interest and efforts of Elsie Quarterman, R. B. Channell, and Louis Bass. A number of the drawings of *Calycocarpum* were made under the supervision of G. K. Brizicky; the remainder, and those of *Cocculus*, were made under that of C. E. Wood, Jr., who has also checked some distributional data, made numerous suggestions, and devoted much time to the manuscript in various stages of completion.

times partly acyclic). Sepals often petaloid, usually 6 (4 to many) in 2 (1–4) series. Petals usually 6 (–9) [4] in 2 (3) series, sometimes glandular or nectariferous. Stamens usually as many as and opposite the petals (or stamens twice as many or more), equal, appearing as 1 or 2 series; filaments sometimes expanded; anthers 2-locular at anthesis, the pollen sacs lateral to ± introrse [or extrorse?], longitudinally dehiscent, sometimes forming narrow valves hinged laterally or at the apex; pollen mostly 3-colpate (spiny in *Diphylleia*). Gynoecium 1-carpellate; stigma various; style present or absent; ovary superior, 1-locular, usually ± gibbous; placenta solitary, parietal or subbasal; ovules anatropous, 2-integumented, mostly ± ascending, the micropyle down, the raphe usually above. Fruit few (1) to many seeded, fleshy or dry, nonfollicular, indehiscent or irregularly ruptured (or transversely [obliquely] loculicidal). Seeds oblong, straight to slightly curved (or ± spherical or disciform-subhemispheric), sometimes arillate; endosperm present; embryo ± straight, usually small (elongate in *Berberis*). (Including Podophyllaceae DC. and *Nandina* Thunb.; excluding *Glaucidium* Sieb. & Zucc. and *Hydrastis* Ellis.) TYPE GENUS: *Berberis* L.

About 10 or 12 genera, variously estimated to include 300 to perhaps over 600 species (*Berberis*, ca. 500 species, *Mahonia*, ca. 100; cf. Ahrendt), mostly in the Northern Hemisphere. The herbaceous species probably amount to fewer than 50. One species in each of five genera is indigenous in the eastern United States; three other genera are indigenous in the western United States. With the exception of *Berberis*, which is represented in both Eurasia and South America, the American genera lack close counterparts in Europe but exhibit strong affinities with vicarious taxa in eastern Asia (Gray), where they also are distributed in deciduous woodlands. At least one species of *Berberis* has been naturalized in our area. One or two other taxa are to be looked for as possible escapes from cultivation.

The conformation of the leaves and, especially, the venation patterns are diverse, but at the generic level more or less palmate venation is frequent, even in the leaflets of pinnately divided leaves. The most conspicuous morphological tendencies uniting Berberidaceae include the calyculate flowers; the multiseriate, deciduous, more or less imbricate perianth; the stamens opposite the petals; and the peculiar, valvelike dehiscence of the anthers of many taxa. The solitary, unicarpellate, nonfollicular gynoecium is a unifying characteristic. The petals in some respects resemble staminodia but are situated in the position of the corolla and are often glandular or nectariferous. The tendency for a multiseriate perianth with more than one series of sepals and of petals places the stamens opposite the petals and the petals opposite the sepals. Sometimes, however, the insertion appears to be slightly acyclic or spiral (see Schmidt) or the stamens may seem to be uniseriate. The opposition of stamens and petals as it occurs in Berberidaceae and Menispermaceae contrasts with the theoretically dissimilar situation in Primulaceae,

Rhamnaceae, etc. (Bentham; see also developmental stages in Payer). In *Berberis*, *Mahonia*, and *Ranzania*, the stamens are tactile, bending inward when touched (Chaveaud, Dop, Kumazawa, and Müller). Initially the anthers are 4-locular and more or less introrse or simply lateral. Later, their orientation may be obscured by somewhat unequal development or by the various modes of dehiscence of the anther wall. In all cases, the anthers are longitudinally dehiscent and more or less 2-locular at anthesis. All of the tissue on the outer side of a locule may function as a single vertical, abaxially hinged valve, as in *Podophyllum*, or as two opposing, laterally hinged valves, as in *Nandina*. In *Ranzania* all of the outer wall of tissue forms an apically hinged valve, while in the remaining genera only a portion of the wall forms a similar but narrower valve (see Kumazawa).

The monomeric nature of the gynoecium (see Eckardt) has been challenged (Chapman, Eames), but the arguments against the older interpretation do not seem always to be convincing. In some clearly teratological examples (*Podophyllum*), more than one ovary of similar structure is formed in the same flower. Although the basic morphology of the gynoecium appears more or less uniform, some of the characteristics of maturation become important taxonomically.

The limits of the higher systematic units of the family are unclear when based exclusively on either floral or vegetative morphology. Subfamily Berberidoideae (including *Mahonia* and *Nandina*) is woody, and the rachis of the imparipinnate (rarely trifoliolate) leaves is either jointed and somewhat swollen at the insertion of the leaflets (or secondary rachises) or, in *Berberis*, the simple leaves are articulated, usually near the base. Subfamily Podophylloideae is herbaceous, usually with scarious ground-level bracts and with scattered vascular bundles in the aerial stems (Agardh, Brown, Harvey-Gibson & Horsman, Metcalf & Chalk). The leaves are simple (sometimes two-parted) and palmately veined or are bi- or trifoliolate or ternately decompound (pinnately compound in *Bongardia*); the rachis of the leaves is not jointed as in Berberidoideae. Although the venation sometimes is obscure and may vary in a single species and among the leaflets on a single leaf, the tendency for palmate or ternate venation is more conspicuous in Podophylloideae than in Berberidoideae. Close morphological relationships among some taxa are clearly evident, but the overlapping of major characteristics seems to prevent the separation of the genera into tribes. For points of view and arrangements of the genera see Heintze, Janchen, Kumazawa, Miyaji, and Tischler.

About 40 named alkaloids have been identified in about eight genera of Berberidaceae (see Willaman & Schubert); of these, about half (20) are reported only for Berberidaceae. Others are reported also for Menispermaceae (9), Ranunculaceae (7), Rutaceae (4), Leguminosae (3); Annonaceae, Monimiaceae, and Papaveraceae (2 each); Aristolochiaceae, Compositae, Lauraceae, Magnoliaceae, and Solanaceae (1 each). Phylogenetic interest naturally focuses on the examples where chemical as well

as morphological similarities are noted. *Hydrastis* and *Glaucidium* are vegetatively similar to some Berberidaceae, but on the basis of floral structure are better referred to Ranunculaceae. Other superficial similarities recall some Papaveraceae and Fumariaceae. The insertion of perianth parts and stamens in Berberidaceae suggests alliance with Menispermaceae and with Lardizabalaceae where the stamens also tend to be opposite the petals. Although phylogenetic relationships among these families are implied, the degree of the relationships is difficult to estimate. In the above instances, it is the solitary, monomeric nature of the gynoecium that clearly distinguishes Berberidaceae. The fruits are neither follicles (in the sense that they do not open longitudinally through the placenta), achenes, nor drupes.

The range of chromosome numbers in the family seems fairly well explored at the generic level, with reports of $2n = 10, 12, 14, 16, 28$, and 56.

The useful properties of some taxa are discussed by Baillon and by Gray; see also genera in *The Merck Index*, ed. 7., 1960, for medicinal and poisonous properties. In some species, the roots or rhizomes and foliage are believed poisonous but the ripe fruits are considered edible (Fernald & Kinsey). No part of the plants should be considered entirely safe for eating, since the family is rich in alkaloids and contains some potentially poisonous compounds. Many taxa are desirable garden plants (cf. *Berberis*).

Some of the exceptional characteristics of taxa not covered in the family description are as follows: in *Achlys* DC., inflorescence spicate, flowers in tight clusters of two or three, perianth absent, stamens several, fruits one-seeded; in *Epimedium* L., petals long-saccate; in *Leontice* L., stipules leafy; in *Leontice* and *Bongardia* C. A. Mey., fruits ± inflated, scarious, and gaping; in *Ranzania* T. Ito, pollen 6–12-rugate; in *Vancouveria* C. Morr. & Decne., filaments ± connivent.

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## KEY TO THE GENERA OF BERBERIDACEAE

General characters: *plants woody or herbaceous perennials; leaves exstipulate, mostly alternate; flowers often calyculate, bisexual, hypogynous, regular; perianth usually of more than 2 series, ± cyclic, mostly 3-merous, fugacious; petals mostly as many (or twice as many) as sepals and opposite the stamens (or stamens twice as many as petals); anthers longitudinally dehiscent, often forming 2 apically hinged valves; gynoecium of a solitary 1-locular carpel; placenta parietal or subbasal; fruit mostly fleshy (rarely loculicidal or ruptured by the young seeds), usually with more than 1 seed.*

A. Plants woody; leaves variously articulated above the base.
  B. Leaves pinnately decompound; inflorescences paniculiform; petals whitish, without distinct glands; anthers longitudinally dehiscent. ..... 1. *Nandina.*
  B. Leaves simple, usually fascicled in the axil of a simple or branched cauline spine; petals yellowish, usually with a pair of adaxial glands; anthers opening by 2 apically hinged valves. ..... 2. *Berberis.*

A. Plants herbaceous, rhizomatous; leaves not articulated.
  C. Flowers solitary on scapes; leaves all radical, 2-foliolate; petals white, usually twice as many as sepals; fruit transversely loculicidal; seeds with a laciniate aril. ..... 5. *Jeffersonia.*
  C. Flowers 1 or more, borne on leaf-bearing stems; petals usually as many as sepals.
    D. Leaves ternately (or apparently pinnately) compound, the leaflets variously veined and lobed; inflorescences racemose; flowers ± greenish to purplish, the petals ± truncate and glandular; seeds globular, mostly paired, on stout funiculi, soon bursting the ovary wall. ..... 6. *Caulophyllum.*

D. Leaves simple, palmately veined and lobed; petals white (or pinkish), rounded and without glands; seeds several in a fleshy fruit.
E. Flowers solitary, usually subtended by 2 ± opposite (rarely alternate), several-lobed leaves; stamens usually twice as many as petals; anthers longitudinally dehiscent. . . 3. *Podophyllum*.
E. Flowers in umbelliform cymes, usually subtended by 2 distinctly 2-cleft, alternate leaves; stamens as many as petals; anthers with 2 apically hinged valves. . . . . 4. *Diphylleia*.

## Subfam. BERBERIDOIDEAE

### 1. **Nandina** Thunberg, Nov. Gen. Pl. 1: 14. 1781.

Evergreen, glabrous shrubs with upright branches, to 2 m. tall. Leaves odd-pinnately decompound, the rachises swollen and articulated both at the insertion of the secondary branches and of the numerous pinnately veined, often reddish, ± sessile, ovate or lanceolate leaflets; petioles persistent, enlarged basally, substipulate and ± clasping. Inflorescences terminal (and axillary), many flowered, paniculiform, determinate, bracteate, the rachises ± scabrous. Perianth multiseriate, mostly 3-merous, the segments coriaceous to scarious and smaller below, ± petaloid and larger above; the lowest 3 segments usually most durable and regularly or irregularly inserted; receptacle elongated. Sepals in about 4 series. Petals in 2 or 3 series, whitish and without distinct glands, ± merging with the sepals. Stamens ± in 1 series; anthers elongate, subsessile, slightly exceeded by the broad connective, longitudinally dehiscent; pollen 3-colpate. Stigma ± 3-lobed; style persistent; placenta parietal; ovules 2 (3 or 4). Fruit globular, coriaceous, usually red and 2-seeded, indehiscent. Seeds ± horizontally oriented, ± disciform, concave-convex with hollow faces adjacent. TYPE SPECIES: *N. domestica* Thunb. (Name derived from a portion of the Chinese for "plant from the south.")

A single species, *Nandina domestica*, heavenly bamboo, $2n = 20$, with many horticultural forms, native to China and perhaps Japan, occurring to an altitude of about 1200 m. An attractive shrub, it is commonly cultivated in the Southeast, where it freely reproduces by seeds in some gardens. It has been found growing without cultivation in Durham County, North Carolina, and should be looked for in other areas as a garden escape.

Although usually classified with Podophylloideae, *Nandina* seems to have no immediate relationship to those herbaceous genera and is here placed with the Berberidoideae because of its woody habit and articulated leaves. The decompound leaves, the graduated multiseriate calyx that more or less merges with the corolla, the anthers without apically hinged valves, the lower chromosome number, and the peculiar seeds distinguish *Nandina* from the *Berberis-Mahonia* complex. The genus sometimes has been considered a separate family, Nandinaceae, but this seems unnecessary. Furthermore, a legitimate family name is not available, since Nan-

dinaceae Horaninow (1834) included the type of Berberidaceae, and Nandinaceae Nakai is a later homonym.

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## 2. **Berberis** Linnaeus, Sp. Pl. 1: 330. 1753; Gen. Pl. ed. 5. 153. 1754.

Evergreen or deciduous, usually spiny shrubs to 2.5 [6] m. tall, with arching branches and yellow inner bark and wood. Leaves simple, ± spatulate, articulated usually near the base, usually ± fasciculate on 1 or more short shoots in the axil of a stout, simple or branched spine [or spine rarely foliaceous or absent]; venation ± pinnately [or palmately] reticulate. Inflorescences axillary, few (1) to many flowered, racemose to subumbellate, terminating short, bracteate shoots. Flowers calyculate; perianth ± yellowish [to reddish orange]. Sepals usually 6, 2[1–4]-seriate, ± petaloid. Petals mostly 6, 2-seriate, usually each with a pair of adaxial glandular regions. Stamens 6; filaments tactile [sometimes ± toothed]; anthers with 2 valves hinged at the apex; pollen 3-colpate. Stigma orbiculate, ± umbilicate; style ± absent [or present]; placenta subbasal; ovules 2–9, erect. Fruit ± oblong, indehiscent, fleshy. Seeds 1–9[–15], without arils; embryo long. (Excluding *Mahonia* Nutt., nom. cons.) LECTOTYPE SPECIES: *B. vulgaris* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 127. 1913. (Name Medieval Latin, apparently from *berbêrys*, presumably the Arabic name of the fruit.) — BARBERRY, BERBERRY.

Perhaps 175 to nearly 500 species, mostly in Asia and South America, poorly represented in North Africa, Europe, and North America. Infrageneric relationships are poorly understood and seem complicated by numerous, presumably interspecific, hybrids. Twenty-one sections were recognized by Schneider, 32 sections by Ahrendt, and 15 series by Rehder. In our area, one species is indigenous, one is naturalized, and one or two others may have escaped from cultivation.

In *Berberis canadensis* Mill. (§ *Sinenses* Schneid.; ser. *Sinenses* Rehd.; § *Canadenses* Ahrendt), American or Allegheny barberry, $2n = 28$, occurring in the mountains of West Virginia and Virginia, southward to

Georgia, and sporadic westward to Missouri (absent from Canada), the leaves tend to be remotely dentate, the petals are apically notched, and the few-flowered racemes often are subumbelliform. In the southwestern United States *B. Fendleri* Gray is somewhat similar. *Berberis* × *Rehderiana* Schneid., of horticulture, is said to be a hybrid between the two. *Berberis Thunbergii* DC. (§ *Sinenses* Schneid.; ser. *Sinenses* Rehd.; § *Tschonoskyanae* Schneid. [cf. Ahrendt]), Japanese barberry, $2n = 28$, naturalized in our area and in much of the eastern United States, is distinguished by its more or less entire leaves, its solitary flowers (or few-flowered umbels), and its immunity to wheat rust. The European *B. vulgaris* L. (§ *Berberis*; § *Vulgares* Schneid.; ser. *Vulgares* Rehd.), $2n = 28$, common barberry, resembling *B. canadensis* but tending to have denticulate leaves, entire petals, and many-flowered racemes, should be looked for in our area, since it is widely naturalized in the Northeastern and the Midwestern States. *Berberis ottawaensis* Schneid. is said to be a hybrid between *B. Thunbergii* and *B. vulgaris*, and *Berberis declinata* Schrad. one between *B. canadensis* and *B. vulgaris*.

The cauline spines of *Berberis*, no doubt the equivalent of leaves, are nearly ubiquitous (sometimes absent), usually obvious, stout, nonarticulated, and variable within the species and also on some plants. In some instances, a fully expanded but nonarticulated leaf is formed, rather than a spine, and in others the spines are soft and soon deteriorate. In any event, the spines, which subtend lateral branches, are distinct in appearance from the scales usually associated with vegetative buds and from the comparable scales also found in some species of *Mahonia*. The simple leaf of *Berberis* seems like a reduction of the more complicated leaves of *Mahonia*, yet the seedling leaves of *Mahonia* probably also are simple. In some taxa of *Berberis* the articulation of the leaves is either subbasal, or midway on the narrowed, petiole-like base of the blade, or distal on a distinct petiole at the base of the expanded blade; and in one (or more) South American species the apparently simple leaves have double articulations, one subbasal and one distal on the petiole.

The separate generic status of *Mahonia* (*Berberis* subg. *Mahonia* Gray and subg. *Trilicina* Gray), which seems to differ consistently from *Berberis* only in its compound leaves (see Ahrendt), is likely to remain debatable. *Mahonia*, however, does not have cauline spines, and the distributional pattern is somewhat more restricted than in *Berberis*. There can be no doubt that *Berberis* and *Mahonia* have much in common, including similar and somewhat unusual pollen, chromosome number, tactile stamens, and susceptibility to wheat rust. The question is whether it is better to treat these two groups of species as separate genera or as an inclusive genus, *Berberis*, with two subgenera. Close affinities between particular species of *Mahonia* and of *Berberis*, which might suggest normal recent pathways of genetic exchange, have not been pointed out, unless this is implied by the several taxa described under × *Mahoberberis* Schneid. (see Ahrendt, Jensen, Levan, Melander & Eade, Vaarama, Wyman). These presumed intergeneric hybrids, with dimorphic leaves, would seem to bridge the gap

between *Mahonia* and *Berberis*, but thus far, only hybrids involving *M. aquifolium* (Pursh) Nutt. are available. The leaves of the elongated shoots of the hybrids tend to be simple and more or less sessile with coarsely spiny margins and are weakly articulated above the insertion on the stem; these leaves seem to be homologous with the prevalent spines of *Berberis*. The leaves of the shorter shoots tend to be trifoliolate, with the rachis articulated at the insertion of the leaflets, the margins of which are less coarsely dentate. The hybrid plants seem to bloom reluctantly and the flowers appear to be sterile. Information regarding the synthesis of hybrids under controlled conditions does not seem to be available.

Chromosome numbers of $2n = 28$ and 56 are reported for *Berberis* and $2n = 28$ for both *Mahonia* and $\times$ *Mahoberberis*. Most species are ornamental, but their cultivation is prohibited unless they are known to be either immune or highly resistant to black stem-rust of wheat (see Fulling). The fruits often are considered edible (Fernald & Kinsey) but should be sampled with caution, since potentially toxic substances occur in the family. In the Southeast, *B. Thunbergii*, *B. Julianae* Schneid., and *Mahonia Bealei* (Fort.) Carr. are commonly cultivated.

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Subfam. PODOPHYLLOIDEAE Lindl.

3. **Podophyllum** Linnaeus, Sp. Pl. 1: 505. 1753; Gen. Pl. ed. 5. 223. 1754.

Herbaceous, rhizomatous perennials to about 50 cm. tall. Solitary leaves ± orbicular, palmately veined, 5–9-lobed, ± centrally peltate, long-petiolate; cauline leaves usually 2 (1–3), ± marginally peltate, 3–7-lobed, short-petiolate, usually subopposite (or alternate), subtending a single flower (rarely 2); juvenile leaves ± quadrate. Hairs unicellular. Inflorescence terminal, of a single, pedunculate, calyculate, ± 3-merous flower. Sepals 6, 2-seriate. Petals 6 or 9, in 2 or 3 series, white (pink). Stamens 12–18 (or more), usually twice as many as petals [or 6 and opposite the petals]; anthers longitudinally dehiscent. Gynoecium normally unicarpellate and solitary (or sometimes of 2–8 free ovaries); stigma convoluted; style indefinite or absent; placenta parietal; ovules numerous. Fruit ± ovate, to 5 cm. long, yellow to reddish orange or purplish, indehiscent, filled with the many seeds and the pulpy placenta, the latter forming ± discreet arils, each inclosing a seed. Seedling cotyledons connate at the base. (Excluding *Dysosma* Woodson.) LECTOTYPE SPECIES: *P. peltatum* L.; typified by the removal of *P. diphyllum* L. to *Jeffersonia* Bart.; see Persoon, Syn. Pl. 1: 418. 1805. (Name from Greek, *podos*, foot, and *phyllon*, leaf; contraction of *Anapodophyllum* Tourn.) — MAY-APPLE, MANDRAKE.

One species in the woodlands and meadows of eastern North America and one (or more) species in Asia. *Podophyllum peltatum*, $2n = 12$, occurs from Florida to Texas, northward to Minnesota, Ontario, and Quebec. The early spring plants are conspicuous, with the terminal

solitary flower bud characteristically placed between more or less paired, reflexed, furled leaves. The arrangement of the leaves and the position of the flower are variable (Foerste, Halsted, Harris, Holm, Wadmond); in exceptional instances the flowering stems lack leaves. The flowers are unusual in having twice as many stamens as petals; occasionally, the flowers have extra or irregularly inserted petals or two or more separate gynoecia (Clute). Eames insists that the normal fruits are the equivalent of three carpels and are only falsely monomeric (see also Chapman). The fruits usually are yellow but sometimes also orange-tinged or reddish; plants with reddish fruits seem to have pinkish petals (Raymond, Steyermark). The rhizomes, which sometimes cause dermatitis when handled, and other parts of the plants, including the green fruits, are bitter and may contain dangerous amounts of "podophyllin," a mixture of potentially poisonous compounds. The ripe fruits, however, are considered edible and sometimes are preserved (Fernald & Kinsey, Muenscher, and Pammel).

In Asia, *Podophyllum emodi* Wall. ex Hook. & Thoms., $2n = 12$, with pink (or white) petals, as many stamens as petals, and reddish fruits, and occurring to an altitude of 4500 m., has the characteristic vernal appearance of the American species, but the cauline leaves (occasionally there are three) are more often alternate and usually are distinctly ternately parted.

The cotyledons of *Podophyllum* are broadly oval or ovate and fused into an elongate, tubular, petiole-like base. During the first growing-season the epicotyl is undeveloped or retarded so that the cotyledons are the only photosynthetic organs. Later, the plumule bursts through the base of the cotyledonary tube, producing first a few bracts and then a peltate leaf with a long petiole (Holm, Dickson, Lubbock). The conformation of the flowering stems in some respects recalls superficially some Ranunculaceae (*Glaucidium*, *Hydrastis*), some Papaveraceae (*Hylomecon*, *Stylophorum*); in our flora, *Podophyllum* vegetatively resembles *Diphylleia*. The relationship of *Podophyllum* to the one or two species of *Dysosma* Woodson, of Asia, is uncertain (see Kumazawa). In *D. pleiantha* (Hance) Woodson (*Podophyllum pleianthum* Hance), the leaves are of a distinctive texture and usually with distinctively toothed margin; the several pendent, usually dark flowers are arranged in an extra-axillary umbel; and the rhizome seems to resemble that of *Diphylleia*. In another taxon of *Dysosma*, the leaves appear to be more or less square and centrally peltate.

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## 4. **Diphylleia** Michaux, Fl. Bor.-Am. 1: 203. *pls. 19, 20.* 1803.

Perennial herbs, to 1 m. tall, from a characteristically jointed rhizome. Solitary leaves reticulately palmately veined, reniform-orbiculate, 2-cleft, to 70 cm. broad, ± centrally peltate, long-petiolate; cauline leaves similar, usually 2, marginally peltate, distinctly alternate. Hairs unicellular. Inflorescence long-peduncled, many flowered, cymose, umbelliform. Flowers 3-merous, noncalyculate. Sepals 6, 2-seriate. Petals 6, 2-seriate, white. Stamens 6; anthers dehiscent by 2 apically hinged valves; pollen conspicuously spiny, ? irregularly aperturate. Style indistinct; placenta parietal; ovules 5 or 6, inserted near the base of the placenta. Fruit ± gibbous, indehiscent, to 1 cm. broad, blue and glaucous. Seeds 2–4, oblong, slightly curved. TYPE SPECIES: *D. cymosa* Michx. (Name from Greek, *dis*, double or twice, and *phyllon*, leaf.) — UMBRELLA-LEAF.

One species along mountain streams in our area from about 1000 to 1700 m. altitude and one or two species in Asia. *Diphylleia cymosa*, $2n = 12$, is distributed in the higher altitudes of northern Georgia, eastern Tennessee, western North Carolina, and adjacent Virginia. The leaves and the inflorescences are sparsely pubescent. In the Asiatic *D. Grayi* F. S. Schmidt, $2n = 12$, the margins of the leaves usually are somewhat less incised, and the pedicels are especially pubescent. The latter taxon, sometimes given varietal status under *D. cymosa*, although that combination seems not to have been formalized, is considered by Li to be a separate species distributed in Japan and Sakhalin, while the Chinese plants, occurring to about 3700 m. altitude in Hupeh, Szechuan, and Yunnan, are referred to *D. sinensis* Li. In the Japanese material, the uppermost leaf tends to be more or less sessile. *Diphylleia* has been attributed, without the citation of specimens, to the Amur region of Manchuria-Siberia (see Kumazawa, Li). The distribution is given in the *Flora of the USSR*, however, as Japan and Sakhalin only.

*Diphylleia* resembles *Podophyllum* and *Dysosma* but is distinguished by the two cleft leaves; the long-peduncled, umbelliform inflorescence; the white petals; the anthers with two uplifting valves; and the spiny pollen.

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## 5. **Jeffersonia** Barton, Trans. Am. Philos. Soc. **3**: 342. *1 pl.* 1793.

Low, acaulescent, glabrous herbs to about 50 cm. tall, from short rhizomes with fibrous, matted roots. Leaves few, radical, subtended by bracts, long-petiolate, the blade deeply 2-parted or 2-foliolate, the parts ± palmately veined [or leaves undivided and ± reniform]. Inflorescence scapiform with a solitary flower (rarely subtended by a linear bract). Perianth 4(3–5)-merous, 3-seriate, often ± acyclic. Sepals 4 (3–5), petaloid, 1-seriate. Petals 8 (9), ± 2-seriate, white [or lavender]. Stamens 8; anthers dehiscent by 2 narrow valves hinged at the apex. Stigma ± 2-lobed; style ± distinct; placenta parietal, the ovules many, indefinite. Fruit ± clavate, ± tuberculate, incompletely transversely [or obliquely] loculicidally dehiscent near the summit, the margins of the stoma becoming extended and ± revolute. Seeds many, oblong; aril laciniate, attached at the upper side of the hilum. TYPE SPECIES: *J. binata* Barton = *J. diphylla* (L.) Pers. (Named in honor of Thomas Jefferson, 1743–1826, Secretary of State under George Washington and third President of

the United States, without "reference to his political character or to his reputation for general science, and for literature," but for his knowledge of natural history, especially botany and zoology.) — TWINLEAF, RHEUMATISM ROOT.

One species in eastern Asia and one in eastern North America, usually in rich deciduous woods. *Jeffersonia diphylla*, $2n = 12$, occurs from Alabama and Tennessee northward to Iowa, Ontario, New York, and Virginia, often in calcareous soil. Frequently there is a minute apiculation at the terminus of the petiole between the two leaflets. The dehiscence of the odd fruits is more or less horizontal. The Asiatic *J. dubia* (Maxim.) Benth. & Hook. ex Baker & Moore (*Plagiorhegma dubium* Maxim.), $2n = 12$, has undivided, slightly apiculate, cordate-reniform leaves, lavender petals, and somewhat obliquely dehiscent fruits.

The unusual features of *Jeffersonia* are the acaulescent habit, flowers with half as many sepals as either petals or stamens, and the definite loculicidal dehiscence of the fruits. Sometimes the insertion of the perianth segments is not quite regular. Both species superficially resemble *Sanguinaria canadensis* L., of the Papaveraceae. The asymmetrical leaflets of *J. diphylla* recall the lateral leaflets of *Achlys*.

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6. **Caulophyllum** Michaux, Fl. Bor.-Am. 1: 204. *pl. 21*. 1803.

Herbaceous, glabrous, rhizomatous perennials. Leaves usually 2 (3), cauline, alternate, the lower 1 (2) ternately (to biternately) or apparently pinnately compound but ± sessile and easily mistaken for 3 leaves (i.e., the common petiole mostly obscure or absent); leaflets 9 or more, variable in shape, the terminal ones ± obovate, ternately lobed or divided, and ± palmately veined; the lateral leaflets sometimes lanceolate and pinnately veined; the uppermost leaf ± similar but smaller. Inflorescence terminal (often with a smaller one axillary), bracteate, several flowered, ± racemose or paniculiform. Flowers yellowish green to purplish, calyculate, 3-merous. Sepals 6, 2-seriate, petaloid. Petals 6, ± uniseriate, small, ±

truncated, glandular. Stamens 6; anthers dehiscent by 2 uplifting valves. Stigma minute, ± introrsely decurrent; style subulate; placenta subbasal; ovules usually 2, on stout funiculi. Fruit soon ruptured by the enlarging seeds, small, thin walled, evanescent. Seeds usually paired, about 1 cm. broad, ± spherical, fleshy, glaucous and blue (easily mistaken for fruits), elevated on conspicuous stout funiculi, and somewhat persistent; endosperm ± spherical, hard, inconspicuously umbilicate ventrally; embryo vertical, central, cylindrical, with radical below. Seedling cotyledons hypogeal. TYPE SPECIES: *C. thalictroides* (L.) Michx. (*Leontice thalictroides* L.). (Name from Greek, *caulos*, stem, and *phyllon*, leaf, in recognition of the peculiar continuity of the stem and leaf.) — BLUE COHOSH, PAPOOSE-ROOT.

One species distributed in eastern North America and another in eastern Asia. *Caulophyllum thalictroides* (*Leontice* subg. *Caulophyllum* Gray; § *Caulophyllum* Prantl), $2n = 16$, occurs in moist deciduous woodlands from New Brunswick and Nova Scotia to Manitoba, and southward, to an altitude of over 1000 m., in the mountains of North and South Carolina, Tennessee, Alabama, and Georgia. The rhizomes contain the alkaloid methylcytisine and perhaps glucosides. The herbage also is bitter, and children should be warned against eating the prominent berry-like seeds. Handling of the plants may cause dermatitis or irritation of mucous surfaces (Muenscher). The roasted endosperm has been suggested as a possible coffee substitute (Gray).

The Asiatic *Caulophyllum robustum* Maxim., $2n = 16$, usually seeming to be more vigorous or larger than our species, occurs to an altitude of about 3500 m. The mostly narrower leaflets more often are pinnately veined.

The unusual leaves, the peculiarly colored flowers, the truncated and glandular petals, and the unique maturation of the seeds are the salient characteristics of *Caulophyllum*. The leaflets and flowers somewhat recall those of *Ranzania japonica* (T. Ito) T. Ito, $2n = 14$, of eastern Asia. Some floral similarities have been noted between *Caulophyllum* and the Eurasian *Leontice* L., having ternately decompound leaves, and *Bongardia* (*Leontice* § *Bongardia* Prantl), having imparipinnate leaves. The seeds in these two, however, do not exceed the finally gaping and scarious ovaries.

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## LARDIZABALACEAE Decaisne, Arch. Mus. Hist. Nat. Paris 1: 185. 1839, "Lardizabaleae," nom. cons.

(LARDIZABALA FAMILY)

About five genera in Asia and two in western South America, probably totaling less than 50 species. One species of *Akebia*, a garden escape, is established in several of the eastern United States.

Among the more common characteristics of the family are the scandent [rarely arborescent], woody habit and perulate buds; the multiple articulation of the alternate, usually palmately [rarely pinnately] compound leaves; the regular, cyclic, trimerous structure of the functionally unisexual [rarely bisexual], hypogynous flowers; and aposepaly, apetaly [or petals reduced], and apocarpy. All or half of the [sometimes monadelphous] stamens are opposite the perianth segments. Although not well exemplified by *Akebia*, the flowers of Lardizabalaceae tend to have two series of sepals and two of petals, so that a sepal subtends a petal, which, in turn, subtends a stamen or staminodium. This pattern also is characteristic of Menispermaceae and Berberidaceae, but contrasts with, for example, Papaveraceae and Fumariaceae, which have only a single series of sepals and conspicuous petals that are not so regularly opposed to as many stamens. Lardizabalaceae are distinguished from Berberidaceae in having unisexual flowers, extrorse anthers, and gynoecia of three or more free carpels. From Menispermaceae they are distinguished in being primarily monoecious [rarely dioecious or bisexual], in having more than a single seed per carpel, and in lacking a bony endocarp. Especially significant in Lardizabalaceae is the submarginal or laminal distribution of the ovules along the ovary wall rather than the restriction of the ovules to a single parietal or subbasal placenta. The fruits of Lardizabalaceae usually are fleshy and more or less follicular [or sometimes baccate] and are considered edible (see Fernald & Kinsey). The plants usually are glabrous [rarely with simple hairs]. Exceptional taxa are *Decaisnea* Hook. f. & Thoms., a hardy, upright shrub or small tree with pinnately compound leaves and bisexual flowers; and *Lardizabala* Ruiz & Pavon, nomenclatural type of the family, which is dioecious. The reported chromosome numbers are $2n = 28$, 30, and 32. Only a few species are cultivated for ornament. In general, the family seems allied with Berberidaceae, Menispermaceae, and Sargentodoxaceae Stapf ex Hutchinson.

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1. **Akebia** Decaisne, Arch. Mus. Hist. Nat. Paris 1: 195. 1839.

Twining, glabrous, deciduous or evergreen, woody vines. Leaves alternate or ± fascicled on short shoots, exstipulate, palmately compound, about 5[3]-foliolate; petioles long, articulated near the base and at the insertion of the petiolules, the latter articulated at the base of the ± elliptical or obovate, ± emarginate, usually minutely apiculate leaflets; blades ± pinnately veined but often with 3 prominent veins from below. Plants monoecious; inflorescences axillary, unisexual or bisexual, bracteate, pedunculate, racemose, or ± subumbelliform. Flowers pedicellate, regular, aposepalous, 3-merous, the sepals usually 3 (6), ± petaloid, brownish or purplish, apetalous, functionally unisexual, hypogynous, apocarpous. ♂ flowers several to many, distal on the raceme (sometimes a few also below); stamens usually 6, free, equal; filaments short; anthers elongate, extrorse, longitudinally dehiscent; pollen mostly 3-colpate; gynoecium rudimentary. ♀ flowers larger, solitary or few; stamens rudimentary; gynoecium of 3–12 free carpels; stigmas ± broad, truncated; style obscure; ovary unilocular; placentae 2, laminal; ovules many, ± orthotropous. Fruits follicular, many seeded, dehiscent along the suture, placenta ± pulpy. Seeds ± arillate?, endosperm present; embryo small. (*Rajania* Houtt. non L.) Lectotype species: *A. quinata* (Houtt.) Decne.; see A. Rehder, Bibl. Cult. Trees Shrubs 166. 1949. (Name derived from the Japanese word for the plant.)

About four species native to eastern Asia. In our area *Akebia quinata*, $2n = 32$, occasionally grown for ornament, apparently is established and growing without cultivation in Madison County, North Carolina. Several authors warn that, if extensively naturalized, this species could become a nuisance by forming dense mats over other vegetation. The number of leaflets sometimes is variable, the terminal one, with slightly longer petiolule, usually somewhat larger. The clusters of slightly fragrant flowers are striking in appearance with their unusual color and velvety texture. The color has been likened to that of raw liver, sometimes appearing maroon; or the sepals of the staminate flowers appear rosy purple and those of the carpellate flowers purplish brown (Anderson). The unusual oblong fruits, to 8 cm. long, seldom seen in cultivation unless the plants are cross-pollinated, are glaucous, purple-violet. When the fruits ripen and open, the seeds are displayed in an elongated, gelatinous pulp derived from the inner portion of the ovary wall. The fruits and roots sometimes are used medicinally in China (Hu).

Another species, *A. trifoliata* (Thunb.) Koidz., $2n = 32$, usually with 3-foliolate leaves and paler sepals and fruits, sometimes also is cultivated. *Akebia* × *pentaphylla* (Mak.) Mak. is said to be a hybrid between this and *A. quinata*.

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MENISPERMACEAE A. L. de Jussieu, Gen. Pl. 284. 1789, "Menisperma," nom. cons.

(Moonseed Family)

Perennial herbaceous vines, woody at least at base [sometimes from tubers, rarely erect shrubs or small trees], sometimes with colorless, bitter juice. Leaves variable, alternate, simple [rarely 3-foliolate], usually exstipulate, the blades mostly palmately [to pinnately] veined, the margin entire to palmately lobed, sometimes peltate, deciduous or evergreen; the petiole sometimes swollen distally and/or basally. Hairs 1- or 2-celled (or multicellular-uniseriate) [sometimes glandular]. Plants mostly dioecious (? sometimes polygamous or flowers tending to be bisexual). Inflorescences variable, commonly supra-axillary, bracteate, usually of many [rarely solitary] flowers, racemose to paniculiform or umbelliform, ± determinate, sometimes concentrated at ends of branches. Flowers mostly small, usually unisexual, usually ± regular (irregular), hypogynous, usually 3(2 or 1)[4 or 6]-merous, greenish, yellowish to whitish, sometimes ± calyculate, the perianth cyclic (to ± acyclic), usually deciduous, aposepalous, apopetalous (sympetalous or apetalous). Sepals 4–9 (or 1) [to many], often in 3-merous cycles, ± 2(3)[or more]-seriate. Petals 6–8 (or 1 or absent), mostly ± 2-seriate. Stamens usually 6 (3, 4) to many [40] in ♂ flowers, often opposite and as many as the petals (or indefinite); filaments free [monadelphous], sometimes embraced by the petals, or anthers sessile on an androphore; anthers 4(? 2)-locular, becoming ± 1(2)-locular at anthesis; pollen mostly prolate (oblate) and 3-colpate (colporate); staminodia often opposite the petals in ♀ flowers. Gynoecium of 3–6 (or 1) [–32] free [to ?partially connivent] carpels, usually in 1 series, often on a gynophore; stigmas various, subulate to laciniate; styles usually short; ovary unilocular, ± gibbous; ovules 1 (or 2), usually inserted ± medially on the solitary parietal placenta, 2-integumented, ± anatropous, descending, the micropyle up (apotropous); gynoecium mostly absent (or rudimentary) in ♂ flowers. Fruits drupes, 1–5 per flower, ± fleshy and indehiscent; endocarp bony, characteristically curved and sculptured, usually laterally compressed; seeds solitary; endosperm present [sometimes ± ruminated or absent]; embryo ± curved, folded or ± cochleate [to straight], molded around a variously shaped ventral intrusion of the endocarp (condyle); cotyledons narrow, ± appressed and fleshy (or foliaceous and laterally displaced) [sometimes unequal]. Type genus: *Menispermum* L.

Perhaps 80 genera and 370 species of tropical and subtropical regions. Four genera and five species are indigenous to the continental United States; four species, representing two tribes, occur in our area.

Among the characteristics uniting most Menispermaceae are the perennial, mostly woody, dioecious, scandent habit; the simple leaves of variable conformation, the blade often with palmate venation and the petiole sometimes swollen distally and sometimes also basally; the perianth tend-

ing to have two series of sepals (sometimes also calyculate) and two series of petals (these often reduced or thickened, sometimes involute or absent) tending to be shorter than the sepals and with each opposite a stamen or staminodium; the apocarpous gynoecium, mostly of more than a solitary carpel, the ovules (usually solitary) medially attached with the micropyle up; and the fleshy, indehiscent fruits with bony endocarp and solitary, usually strongly curved, folded, or somewhat coiled seeds.

The vascular bundles of young stems are separated by broad medullary rays. The wood is distinctive, with secondary thickening from fascicular or extrafascicular cambia, sometimes forming concentric or eccentric rings of bundles, resulting in many cambia and alternating layers of xylem and phloem (see Metcalf & Chalk and Esau). Within a taxon, the leaves often vary from entire to lobed, nonpeltate to peltate. The matching of the dioecious materials and the determination of sterile specimens often is difficult. Correlations between taxa resembling one another in the anatomical structure of the swollen portion of the petiole (which differs from the remainder of the petiole) and taxa resembling one another in fruit and seed characters have not been found (Rudolph, fide Metcalf & Chalk). Most of the hairs that seem to be unicellular probably are bicellular, the basal cell inconspicuous. The lack of tubers in our species should be verified.

The (anatropous) ovules at first seem more or less straight and vertical, the micropyle up. During the maturation of the endocarp or stone, the placental region seems to buckle inward towards the seed, leaving a notch or hollow exteriorly and forming inwardly an intrusion, or condyle (Miers), of various proportions around which the seed and the embryo are curved. The condyle in tribe Menispermeae is seen superficially as a depression (nearly orbicular in *Menispermum*, excentric in *Cocculus*, or narrowly obovate in *Cissampelos*) on the broad faces of the laterally compressed endocarps bordered adaxially by a notch or indentation on the margin of the endocarp. Internally the condyle may be hollow, perforated, or reduced to a narrow, partial partition of the seed.

Although the shape of the fruits may be nearly spherical, abaxial deformation of the endocarp often is accompanied by extreme abaxial enlargement of the pericarp, so that the final position of the style (and the apex of the seed) is subbasal in tribe Menispermeae. Abaxially, a median-longitudinal line or crest is characteristic of many endocarps; adaxially the crest often is obscured by the condyle. Insight into the form of the closed condyles of tribe Menispermeae may be provided by the broad, open concavity of the endocarp of *Calycocarpum* (tribe Tinosporeae) with its conspicuous median adaxial crest.

Menispermaceae, distinguished by habit, dioecism, position of micropyle, drupaceous fruits, and curved seeds, resemble Berberidaceae and Lardizabalaceae in the insertion of perianth (petals often reduced) and androecium, and in the apocarpous gynoecia. Flowers of Berberidaceae, however, are bisexual, and the solitary carpels usually develop more than one seed, attached to a single parietal or subbasal placenta, apparently with

the micropyles down. In Lardizabalaceae, the plants usually are monoecious (otherwise dioecious), the flowers unisexual, the ovules submarginal in more than one vertical row, and the leaflets of the compound leaves articulated with the rachis.

The family customarily has been divided largely on characteristics of the fruits (endocarp) and seeds (endosperm and embryo). Originally six (later seven) tribes were recognized by Miers, five tribes by Hooker & Thomson, four series by Baillon, four tribes by Prantl, and, most recently, eight tribes by Diels. In each case, the genera were rearranged to some extent. In Diels's treatment, the three largest tribes (comprising over 80% of the species and of the genera) are Triclisieae Diels (14 genera, 96 species), lacking endosperm; Tinosporeae Hook. & Thoms. (41 genera, 78 species), having endosperm and thin, laterally displaced foliaceous cotyledons; and Menispermeae (Cocculeae Hook. & Thoms.) (16 genera, 140 species), having endosperm and appressed, nonfoliaceous cotyledons.

Menispermaceae in our area are but the fringes of a large, complex family. When classified according to conformation of endocarps and embryos, *Cocculus* (*q.v.*), *Menispermum*, and *Cissampelos* (all of tribe Menispermeae), seem relatively similar, while *Calycocarpum* (tribe Tinosporeae), seems remote. A classification based upon floral morphology, however, would lessen the apparent isolation of *Calycocarpum* and emphasize the distinctness of *Cissampelos* (*q.v.*), with its strongly dimorphic flowers.

About 90 named alkaloids have been identified in about 29 genera of Menispermaceae (see Willaman & Schubert); of these, about three-fourths (ca. 68) are reported for Menispermaceae only. Others occur also in Berberidaceae (9), Fumariaceae (6), Rutaceae (6), Ranunculaceae (5), Lauraceae (5), Monimiaceae (3); Papaveraceae, Magnoliaceae, Annonaceae, and Buxaceae (2 each); and Aristolochiaceae and Hernandiaceae (1 each).

The poisonous and medicinal properties of Menispermaceae are discussed by Baillon. Commercial curare (Intocostrin), for medicinal use, is prepared from a species of *Chondodendron* (Merck Index, ed. 7. 1960). Portions of some taxa are used for aboriginal poisons and sometimes, with potentially dangerous consequences, for fish poisons, pesticides, or bitter flavorings. Only a few species of the family are cultivated for ornament.

Chromosome numbers of $2n = 18, 20, 24, 26, 38, 48, 50, 52, 54$, and 78 have been reported from among about ten genera.

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## Key to the Genera of Menispermaceae

General characters (see *Cissampelos*): *dioecious vines, woody at base; leaves exstipulate, alternate, petiolate, palmately veined, entire to lobed; flowers unisexual, hypogynous, usually regular (irregular), often calyculate; sepals 2(or more)-seriate (or 1); petals reduced, ± 2-seriate (or 1, sympetalous, or absent); stamens free, often opposite and embraced by the petals (or anthers sessile on an androphore); anthers longitudinally (or horizontally) dehiscent; gynoecium apocarpous, of (1) 3–6 carpels; ovules usually solitary (or 2), the micropyle up; fruits drupaceous, the endocarp bony, characteristically shaped, often sculptured; 1-seeded; embryo usually curved or folded.*

A. Plant bearing only ♀ flowers.
  B. Perianth of 1 sepal opposite 1 petal; gynoecium of 1 pubescent carpel; peduncles unbranched, several in the axil of a broad bract; fruit red, pubescent, the style subbasal; stone orbicular, laterally compressed, sculptured (subtropical Florida). . . . . 4. *Cissampelos*.
  B. Perianth of 6 or more segments; gynoecium of 3 or 6 glabrous carpels; peduncles branched, minutely bracteate.
    C. Petals apparently absent; sepals glabrate, usually each subtending two short, unequal staminodia; carpels 3, stigmas irregularly laciniate, extrorsely radiate; gynophore inconspicuous; fruits black, the style apical; stone + smooth, broadly cup shaped and adaxially toothed. . . . . 1. *Calycocarpum*.
    C. Petals present, shorter than the sepals; fruits with style subbasal; stone sculptured, laterally compressed.
      D. Carpels 3, stigmas extrorsely dilated and convolute; gynophore mostly longer than broad; sepals glabrate; fruits glaucous, blue-black, sessile on the 2–3 mm. long gynophore; stone crescent shaped. . . . . 3. *Menispermum*.
      D. Carpels 6, stigmas subulate; gynophore broader than long;

sepals coarsely pubescent; fruits red, short-stipitate on an inconspicuous gynophore; stone appearing coiled. 2. *Cocculus*.

A. Plant bearing only ♂ flowers.
  E. Anthers 4, sessile on a short androphore, the dehiscence horizontal; sepals 4, coarsely pubescent; corolla sympetalous. . . . . 4. *Cissampelos*.
  E. Anthers 6 to many, filaments free; sepals more than 4.
    F. Stamens 12 or more; sepals glabrous or glabrate.
      G. Anthers included, introrse, oblong, 2-locular at anthesis, the dehiscence vertical. . . . . 1. *Calycocarpum*.
      G. Anthers exserted, ± apical, 4-lobed, erect, ± 1-locular at anthesis, the dehiscence ± confluent apically. 3. *Menispermum*.
    F. Stamens 6, anthers included, ± apical, 4-lobed, nodding inward, ± 1-locular at anthesis, dehiscence ± confluent apically; each filament embraced by a petal; sepals coarsely pubescent. . . . . 2. *Cocculus*.

Tribe TINOSPOREAE Hook. f. & Thoms.

1. **Calycocarpum** Nuttall ex Gray, Gen. Pl. U. S. 1: 75. *pl. 30*. 1848.

Leaves thin, deciduous, not peltate, usually 5(7)-veined, 3–5–7-lobed; petiole often longer than blade. Hairs mostly multicellular-uniseriate. Flowers regular, ± calyculate with 1–3 small sepal-like bracts. Sepals 6, ± petaloid, 2-seriate, ± equal, glabrate. ♂ flowers: petals absent; stamens about 12, arrangement ± indefinite, not enfolded by perianth segments; filaments free; anthers included, ± introrse, attached subapically, 2-locular at anthesis, longitudinally dehiscent; pollen prolate, 3-colpate (colporate). ♀ flowers: petals apparently absent; staminodia 12, narrow, short, thick, unequal, 2 opposed above each sepal (the lower staminodia probably equivalent to petals); gynophore inconspicuous; carpels 3 (4); stigma extrorsely reflexed, irregularly laciniate, conspicuous; style short; ovules apparently solitary. Fruits 1–3 per flower, black, ± ovoid, ca. 25 mm. long, the style apical, the gynophore inconspicuous; endocarp large (to ca. 20 mm. long, 15 mm. wide), ovoid-cup-shaped, ± smooth abaxially, broadly concave adaxially and toothed, ± mucronate apically; embryo broadly curved, the cotyledons foliaceous, laterally displaced. TYPE SPECIES: *C. Lyonii* (Pursh) Gray. (Name from Greek, *calyx*, a cup, and *carpos*, fruit.) — CUPSEED, LYONIA-VINE.

Monotypic, distributed in rich or alluvial soils, in thickets, woods, or river banks, from northwestern Florida and western Georgia, northward to Tennessee, Kentucky, and southern Illinois, and westward to eastern Kansas (?), eastern Oklahoma, and Texas.

The thin, nonpeltate leaves with petioles at least as long as the blades are notable. The blades, to ca. 25 cm. long and wide and usually with five or more veins, are deeply three or more lobed to near the center of the blade with the lobes narrowed basally. The flowers of both sexes seem to be apetalous. In the staminate, the included, introrse, finally two-locular anthers are distinctive. In the carpellate, two reduced staminodia are opposed above each sepal; the lower series of staminodia, apparently

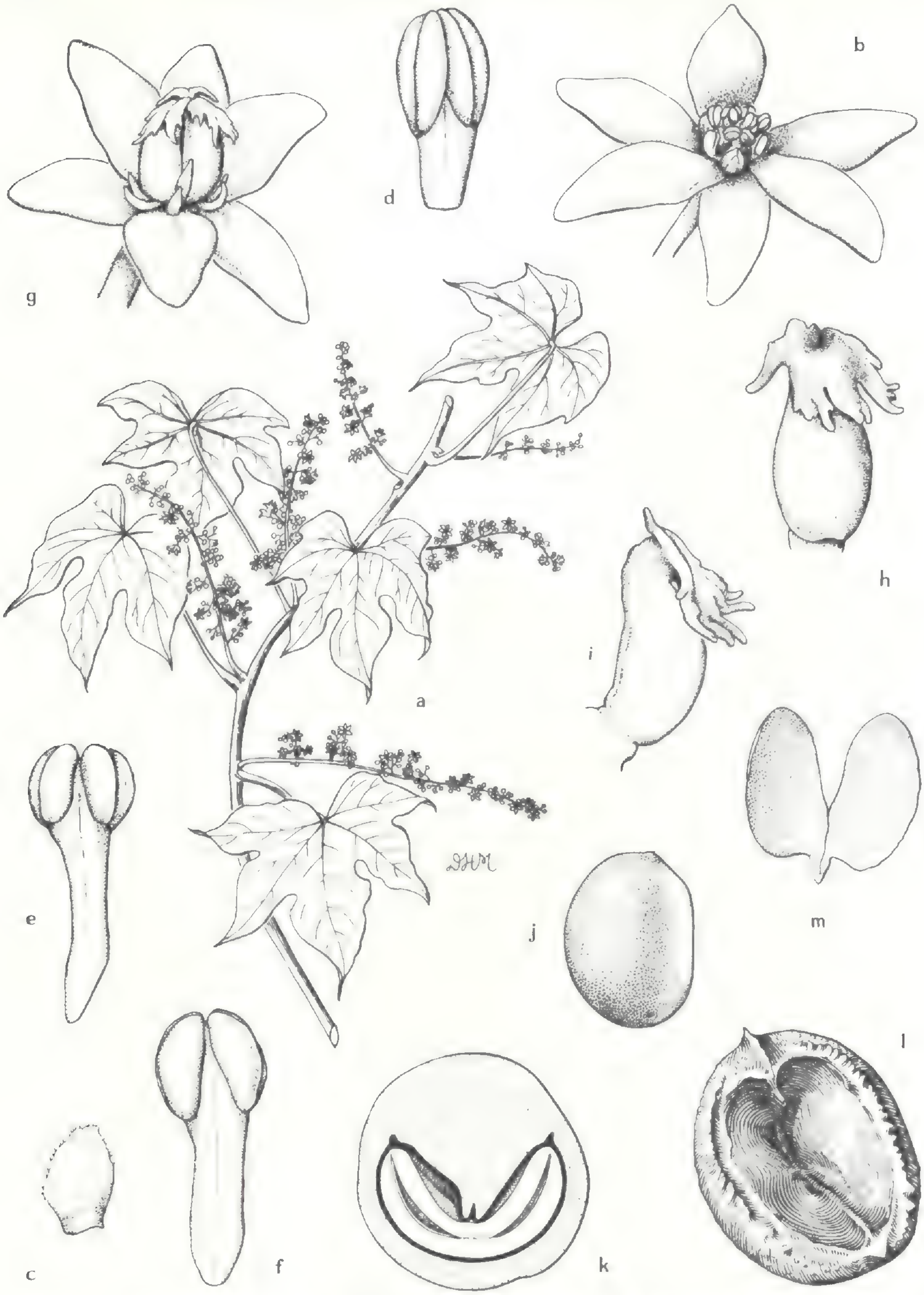


FIG. 1. **Calycocarpum.** a–m, *C. Lyonii*: a, portion of flowering staminate plant, × ¼; b, staminate flower, showing stamens and two series of sepals, × 8; c, sepal-like bractlet from calyculus of staminate (or carpellate) flower, × 20; d, outer stamen, adaxial side, × 20; e, f, inner stamens, adaxial side, × 20; g, carpellate flower, showing sepals, staminodia, and carpels, × 8; h, carpel, abaxial side, showing irregularly laciniate stigma, × 16; i, carpel, lateral view, showing stigma and short gynophore; j, mature drupe, showing terminal stigma-style, × 1; k, semidiagrammatic cross section of fruit, showing foliaceous cotyledons of embryo surrounded by endosperm (white), bony endocarp (black), and fleshy fruit wall, × 2; l, endocarp, adaxial side, × 2; m, embryo, × 2.

missed by Gray, were called petals by Miers and Diels. In texture and appearance, these organs resemble staminodia more than petals, but are in the appropriate position for petals. Unlike other Menispermaceae in our area, the style remains apical in the fruit, and the ovoid endocarps are smooth and not laterally compressed. While the embryo is not so tightly curved as in tribe Menispermeae, it is broadly so, conforming to the wide, open adaxial depression of the condyle.

REFERENCES:

Under family references see GRAY and MIERS.

2. **Cocculus** A. P. de Candolle, Syst. Nat. 1: 515. 1817 ("1818"), nom. cons.

Leaves ± coriaceous, the blades mostly longer than the petioles, nonpeltate, prominently 3-veined (often with a finer submarginal vein at either side), deltoid to ovate, sometimes 3- or 5-lobed, often apically mucronulate, basally oblique to cordate. Hairs 1- or 2-celled. Flowers ± regular, calyculate with 1–3 small sepal-like bracts. Sepals 6, ± pubescent, 2-seriate, the inner 3 larger, the margins ± fimbriate to erose. Petals 6, ± 2-seriate, shorter than the inner sepals, ± fleshy [bifid], each embracing a stamen or staminodium. ♂ flowers: stamens 6, free, included, usually nodding inward; anthers 4-lobed, appearing terminal, ± 1-locular at anthesis, dehiscence ± apically confluent; pollen prolate, 3-colpate (?colporate). ♀ flowers: staminodia 6, ± linear; gynophore distinct, broader than long; carpels 6, in 1 series; stigma ± subulate, terete, turned outward, grooved along the upper surface; style short. Fruits 3–5 per flower, red [purple], glabrous, short-stipitate (–1 mm.), the style subbasal, the gynophore inconspicuous (less than 1 mm. long); endocarp sculptured, appearing coiled, laterally compressed, shallowly notched adaxially, the radicular end slightly projecting; embryo ± coiled, the cotyledons appressed, narrow (but wider than the radicle). LECTOTYPE SPECIES: *C. hirsutus* (L.) Diels (*Menispermum hirsutum* L.), typ. cons.; see Rickett & Stafleu, Taxon 8: 271. 1959, and Int. Code Bot. Nomencl. 1961: 259. (Name from Greek, diminutive of *coccos*, berry; originally applied to "Cocculus indicus" [*Menispermum Cocculus* L. = *Anamirta Cocculus* (L.) Wight & Arn.]) — SNAILSEED, MOONSEED.

About 11 species, mostly of warmer regions, eight in the Old World, two in North America, and one in Hawaii; the conserved type species is native to Africa.

*Cocculus carolinus* (L.) DC. (*Menispermum carolinum* L., *Cebatha carolina* (L.) Britt., *Epibaterium carolinum* (L.) Britt.), coralbeads, Carolina moonseed, $2n = 78$, is distributed in woods, thickets, and fields from Florida to Texas northward to Kansas, Indiana, Virginia, and North Carolina, and in Mexico, from Coahuila to Tamaulipas. The nonpeltate leaves with three prominent veins, the blades to ca. 14 cm. long and wide; the pubescent sepals; the included stamens, each embraced by a petal;

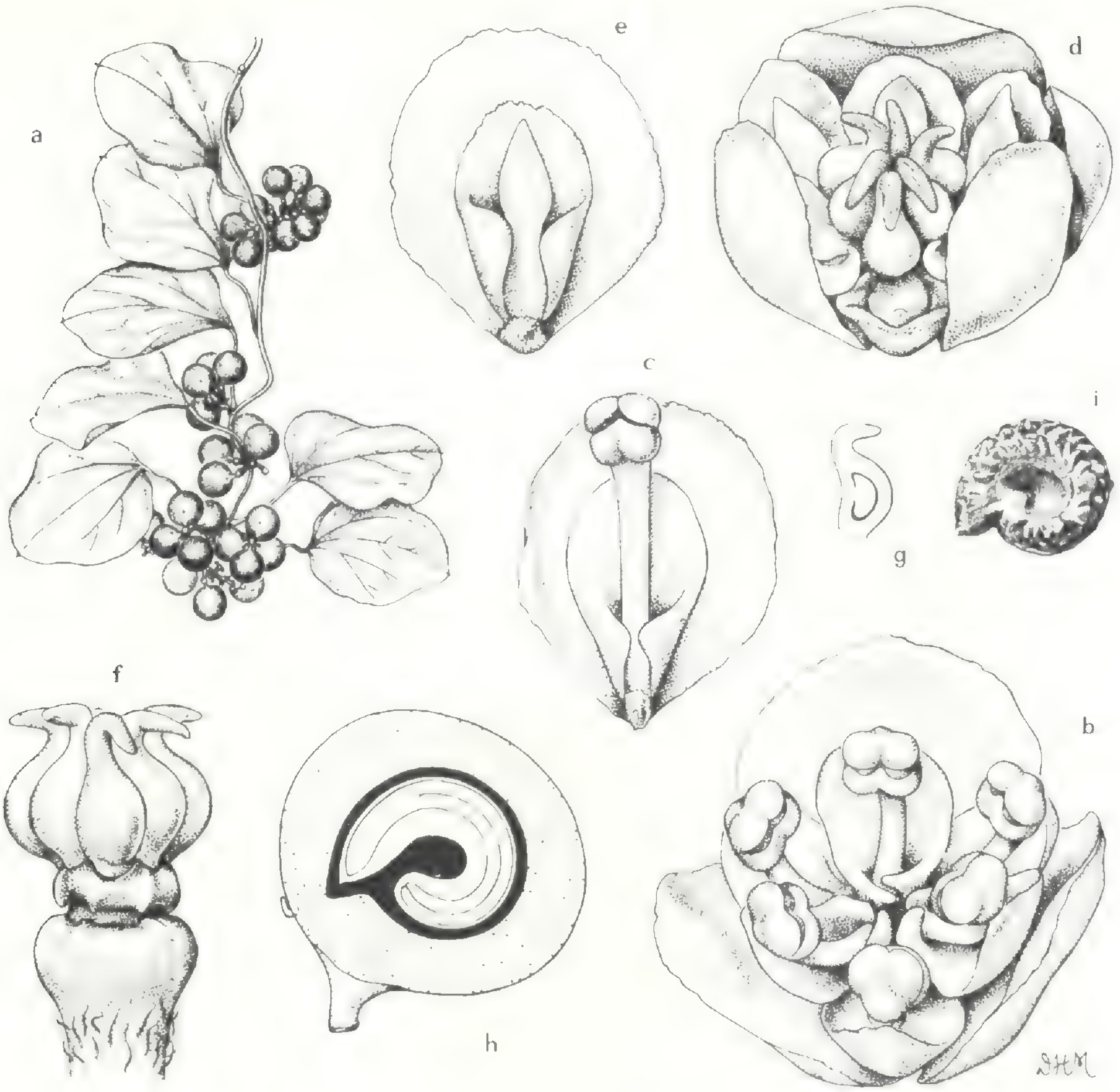


FIG. 2. **Cocculus.** a–i, *C. carolinus*: a, pendent branch with fruit, × ½; b, staminate flower, showing inner sepals, two series of petals and stamens, the short outer sepals not visible, × 15; c, inner sepal, clasping petal, and stamen, showing dehiscence of anther, × 15; d, carpellate flower, outer sepal in foreground removed to show inner sepals, two series of petals, staminodia, and carpels, × 15; e, inner sepal, clasping petal, and staminodium, × 15; f, carpellate flower, with perianth and staminodia removed to show receptacle, gynophore, and gynoecium of gibbous carpels with reflexed, subulate stigmas, × 15; g, diagrammatic vertical section of carpel, showing attachment of ovule, the micropyle up, × 10; h, diagrammatic vertical section of fruit, showing stipitate base, subbasal stigma-style, coiled embryo surrounded by endosperm (white), bony endocarp (dark), and fleshy fruit wall, × 4; i, subhelical sculptured endocarp, showing central depression of condyle, the micropyle to the lower left, × 3.

the short, broad gynophore; and the glabrous, short-stipitate, red fruits with somewhat coiled endocarp are distinctive. The closest affinities may lie with some portion of the complex involving *C. trilobus* (Thunb.) DC., of eastern Asia, although in the latter the petals are ligulate and bifurcate and the fruits dark purple.

West of our area, *Cocculus diversifolius* DC., having leaves with short

petioles and often narrow, oblong blades with revolute margins, and dark purple fruits, occurs in Texas and Arizona, and southward, in Mexico, to Oaxaca.

While the taxa of *Cocculus* primarily are scandent (resembling *Menispermum*), *C. laurifolius* DC., $2n = 26$, of Southeast Asia, sometimes cultivated in the warmer parts of the United States, is an upright shrub or small tree with glossy leaves. In Socotra, *C. Balfourii* Schweinf., also shrubby, is conspicuous for its extra- or supra-axillary, flattened, sometimes branched cladodes on which are borne the flowers and fruits. *Cocculus* and *Menispermum* were placed in subtribe Menisperminae (Coccu-linae Hook. & Thoms.) by Diels, but Miers( see p. 114. 1871) separated them, placing *Cocculus* in his tribe "Platygoneae."

Chromosome numbers of $2n = 18$, 20, 22, 26, 38, 50, 52, and 78 are reported.

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3. **Menispermum** Linnaeus, Sp. Pl. 1: 340. 1753; Gen. Pl. ed. 5. 158. 1754.

Leaves ± coriaceous (or thin), usually ± peltate (nonpeltate); blade usually 5(or more)-veined, cordate, or deltoid to reniform in outline, shallowly to deeply ± 5–7(3–9)-lobed or pointed (or unlobed), often apically mucronulate, the petioles at least as long as the blades. Hairs 1- or 2-celled. Flowers ± regular and calyculate with 1 or 2 small sepal-like bracts; insertion of perianth and stamens or staminodia sometimes ± acyclic. Sepals 6 (4–10), entire to ± erose, ± 2-seriate. Petals 6–9, ± fleshy, the margins ± involute, often nearly equalling the sepals. ♂ flowers: stamens (9) 12–24, exserted, filaments erect, sometimes ± embraced by the petals; anthers 4-lobed, appearing terminal, ± 1-locular at anthesis, the dehiscence ± apically confluent; pollen prolate, 3-colpate. ♀ flowers: petals not embracing the staminodia, spatulate, somewhat larger than in ♂ flowers; staminodia (4) 6–12, ± filiform, variously inserted or 1-seriate and opposite the petals, the rudimentary anthers introrse; gynophore distinct, longer than broad; carpels 3; stigmas extrorsely dilated, ± convolute; style short, reflexed. Fruits 1 or 2 per flower, black, glaucous, nonstipitate, the style subbasal, the gynophore 2–3 mm. long; endocarp sculptured, broadly crescent shaped, laterally compressed, conspicuously notched adaxially; embryo broadly crescent

shaped, the cotyledons appressed, narrow, no wider than the radicle. LECTOTYPE SPECIES: *M. canadense* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 131. 1913. (Name from Greek, *mene*, moon, and *sperma*, seed.) — MOONSEED.

One species of eastern Asia and one of thickets, woods, stream banks, and hedgerows in eastern North America. Many species originally described in *Menispermum* now are placed in other genera.

*Menispermum canadense* L., $2n = 52$, is distributed from southeastern Manitoba to Quebec, southward to western North Carolina, northern Georgia, northwestern Florida, ?Alabama, Tennessee, Arkansas, and Oklahoma. The leaf blades tend to be peltate, rather thin, mostly with five or more veins, and the petioles at least as long as the blades. Among other distinguishing characteristics are the glabrate sepals, the exserted stamens, the relatively long gynophore, and the nonstipitate, black fruits. Plants referred to *M. mexicana* Rose, occurring disjunctly in Nuevo León, Mexico, with leaves varying from peltate to nonpeltate, probably are conspecific with *M. canadense*. Our species somewhat resembles *Cocculus carolinus* vegetatively, but the leaves of the latter are nonpeltate and tend to have only three prominent veins. In eastern China and Japan, *M. dahuricum* DC., $2n = 52–54$, resembles our species, but the leaves seem more strongly peltate. The fruits, looking like grapes, are bitter and probably poisonous.

The taxonomy of *Menispermum* has been complicated by lack of agreement on the proximity of *Cocculus* and *Cissampelos*, but is simplified to the extent that the name of the tribe and subtribe must be formed on the root *Menisperm-*. Miers, placing *Cocculus* in another tribe, divided the Menispermeae ("Leptogoneae") into subtribes Menisperminae and Cissampelineae (see *Cissampelos*). Tribe Cocculeae of Hooker & Thomson and of Diels included both *Menispermum* and *Cocculus*. In addition to the differences in floral structure, the stones and embryos of *Menispermum* are broadly crescent shaped, while those of *Cocculus* appear somewhat coiled.

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4. **Cissampelos** Linnaeus, Sp. Pl. 2: 1031. 1753; Gen. Pl. ed. 5. 455. 1754.

Leaves ± coriaceous, ± broadly reniform (to ovate or suborbicular), often apically emarginate, mucronulate [sometimes peltate], usually with 5 or more veins. Hairs 1- or 2-celled. Flowers minute, symmetrically

dimorphic; perianth pubescent [glabrous], not calyculate. ♂ flowers: regular; sepals 4, valvate; corolla sympetalous [? or of 2–4 free petals]; anthers about 4 [? to 8 or more], extrorse, included, uniseriate, sessile on a short, central, columnar androphore, ± 1-locular at anthesis, the dehiscence horizontal; pollen ± oblate, 3-colpate. ♀ flowers: irregular; sepal 1; petal 1 [sometimes divided], opposite the sepal; staminodia absent; gynoecium of a solitary carpel; stigma 3-parted; style short, erect; ovary pubescent [glabrous]; ovules 2, the placenta toward the perianth. Fruit red, pubescent [glabrous], nonstipitate, the style subbasal; endocarp sculptured, ± orbicular, laterally compressed, minutely notched adaxially; embryo ± conduplicate, the cotyledons appressed, narrow, no wider than the radicle. LECTOTYPE SPECIES: *C. Pareira* L.; see Britton & Millspaugh, Bahama Fl. 142. 1920. (Name from Greek, *cissos,* ivy [*Hedera*], and *ampelos*, grape [*Vitis*].)

Number of species uncertain, perhaps 20 to nearly 70, widely distributed in warmer regions.

Pantropical and perhaps the most widely distributed taxon of Menispermaceae (cf. Diels), *Cissampelos Pareira*, $2n = 24$, is known in our area from Dade County, Florida. The plants are reported to be high climbing. The leaf blades seem to be nonpeltate, somewhat reniform, with five or more veins, and the petioles at least as long as the blades; in other areas the blades sometimes are ovate and peltate. The carpellate flowers are borne in the axils of usually broad, relatively large bracts resembling small, thin, leaves on peculiar inflorescence branches. Several flowers, each on a separate, stout, upright, unbranched peduncle, these apparently arranged in two parallel ranks, are clustered in the axil of each bract. The bracts are variable in size but often equal or exceed the flowers and, later, the pubescent, red fruits; bractlets seem to be absent. The stones are nearly orbicular, with only a minute adaxial indentation; externally, the condyle appears obovate, and the embryo is strongly folded or horseshoe shaped. The staminate flowers are borne in very finely branched inflorescences with a few bracts and bractlets of various sizes; many of the filiform pedicels are ebracteate. The number of locules in the anthers before anthesis is not apparent.

Floral dimorphism is especially conspicuous in *Cissampelos*, with the regular, sympetalous staminate flowers having a symmetrical androphore, and the irregular carpellate flowers composed of a solitary sepal, petal, and carpel. The general shape and sculpturing of the endocarps seem relatively similar to those of *Cocculus,* and especially *Menispermum*, but the floral morphology is distinctive; consequently, the systematic position of *Cissampelos* seems somewhat unclear. Miers placed *Cissampelos* (along with four other genera) in the subtribe Cissampelineae ("Cissampelideae"), one of his two subtribes under Menispermeae ("Leptogoneae"), approximating the later treatment of Diels who, however, divided the Menispermeae ("Cocculeae") into three subtribes. Hooker & Thomson placed *Cissampelos* in their tribe Cissampelideae.

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# A PROPOSED EXPLANATION FOR THE ORIGIN OF COLCHICINE-INDUCED DIPLOID MUTANTS IN SORGHUM [1]

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COLCHICINE, AN ALKALOID extracted from plants of *Colchicum* species, especially *C. autumnale* L., has long been used for medicinal purposes. In tissues of animals which have been exposed to the drug, mitoses are arrested with the result that some cells are produced with a doubled number of chromosomes (Eigsti & Dustin, 1955, Chap. 1). Botanists realized that such tetraploid cells in plant tissues might give rise to tetraploid shoots and plants, and this proved to be the case (Blakeslee, 1937; Nebel & Ruttle, 1938). In many plant species, colchicine treatment has been used successfully to produce polyploids for cytogenetic research and for breeding programs (Eigsti & Dustin, 1955, Chap. 11).

In the breeding program at South Dakota State College, colchicine treatment of *Sorghum* was found to produce, in addition to polyploids, diploid mutant plants changed for many characters. When the mutants were selfed, some produced uniform progenies and continued to breed true in succeeding generations; others produced progenies which segregated for many characters (Franzke & Ross, 1952).

'Experimental 3' (FIG. 1), which has given rise to many colchicine-induced diploid mutants, has been studied more extensively than other lines. It was developed from crosses involving three sorghum lines: 'Day Milo', a grain sorghum (*Sorghum vulgare* Pers. var. *subglabrescens* (Steud.) A. F. Hill); 'Black Amber Cane', a sorgo (*S. vulgare* var. *saccharatum* (L.) Boerl.); and Sudan Grass, a grass sorghum (*S. sudanense* (Piper) Stapf). Two crosses, 'Day Milo', with 'Black Amber Cane' and 'Day Milo' with Sudan Grass, were made in 1932. An early dwarf grain type was obtained from each of these crosses by repeated selfing and selection. These two types were crossed together in 1939, and from the progeny of this cross, 'Experimental 3' was developed by continued selfing and selection. It had been through eight generations of selfing and was true-breeding when the first mutants were obtained in 1948. After more than 20 generations of selfing, it is still apparently the same true-breeding

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line and continues to give rise to colchicine-induced diploid mutants some of which resemble one of the original parents. For example, there are mutants with slender stems, narrow leaves and open panicles (Class I, Franzke & Sanders, in press) similar to Sudan Grass. Except where otherwise specified, the following discussion relates to sorghum line 'Experimental 3' and its derivatives.

This paper brings together the results of research on colchicine-induced diploid mutants in *Sorghum* and, in the light of available information, proposes a new hypothesis to explain their origin. The significance of the hypothesis, if proved valid, is also considered.

## COLCHICINE TREATMENT OF SORGHUM LINE 'EXPERIMENTAL 3'

Sorghum plants are treated with colchicine at the seedling stage. Shortly after germination, a mixture of 0.5 per cent colchicine in lanolin, heated to the melting point, is applied to cover the coleoptile. Treated seedlings have been planted in various media and kept under various conditions in greenhouse, laboratory, or rooms with controlled light and temperature. Both polyploids and diploid mutants have been obtained in the treated generation. There are indications that environmental conditions may influence the outcome of treatment.

### Polyploids

Experimentally produced polyploids of 'Experimental 3' are, for the most part, tetraploid plants which exhibit the same qualitative characters as diploid plants, but are shorter and stockier with broader stems, heavier leaves, larger glumes and grain, and have a high degree of sterility. These characteristics are similar to those of polyploids in many other plant species. Self-progenies of these polyploids frequently include both diploid and polyploid plants, indicating that the treated plants were chimeras. The incidence of induction of polyploids, which has been as high as four out of 15 surviving treated seedlings, appears to be increased by conditions which favor the growth of treated seedlings (Franzke *et al.*, 1960).

### Diploid Mutants

Diploid mutants exhibit qualitative and quantitative characters which are radically different from those of 'Experimental 3' plants. Yet, the changes have been brought about by colchicine after the germination of an 'Experimental 3' seed. Uniform self-progenies of two diploid mutants are shown in FIGS. 2 and 3; each plant repeats the characters of the original mutant. A segregating self-progeny of a nontrue-breeding mutant is shown in FIG. 4. In progenies of this kind, most characters may segregate, or some may segregate while others do not (Sanders *et al.*, 1962). Thus, colchicine-induced diploid mutants may be true-breeding, nontrue-breeding, or intermediate between the two conditions. The incidence of induction of diploid mutants, especially true-breeding ones, which has been as high as

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four out of nine surviving treated seedlings, appears to be increased by conditions which retard the growth of treated seedlings (Franzke *et al.*, 1960). The largest proportion of mutants among surviving treated plants was obtained under conditions which almost eliminated survival. Maintaining treated seedlings at a lower temperature (68° F.) increased survival while still permitting induction of mutants (Sanders *et al.*, 1960).

Some types of true-breeding mutants were found to recur thereby forming classes of almost identical mutant lines (Franzke & Sanders, in press). Some classes included as many as ten lines, most of them obtained within a five-year period of experimentation. Three lines from one class were intercrossed in all possible combinations and were each crossed to 'Experimental 3'. The results indicated that these three mutant lines were genotypically as well as phenotypically alike (Chen *et al.*, 1961).

The original hypothesis proposed for the origin of the diploid mutants was "that such variant plants could originate through reductional grouping of the somatic chromosomes so that a concentration of chromosomes containing gene blocks originating from one of the ancestors of the polyploid species might occur in one cell" (Franzke & Ross, 1952).

When no irregularities were detected in chromosome-pairing relationships at pachytene in mutants or in $F_1$ plants from crosses between mutants and other lines including parental ones, the original proposal was discarded. It was then concluded "that no detectable rearrangement of chromatin occurred," and "that the colchicine-induced variants have resulted from gene mutation or cryptic structural changes in the chromatin" (Harpstead *et al.*, 1954). Genetic studies of one of the mutants led to an estimate that "at least 12 (in all probability more) immediate mutations for the characters studied" had occurred (Foster *et al.*, 1961).

Current information, however, suggests that the origin of the mutants is more similar to the first proposal since the variations in them resemble major chromosome changes more than individual gene changes, despite the lack of confirming cytological evidence.

## PRESENT HYPOTHESIS FOR THE ORIGIN OF DIPLOID MUTANTS

It is now proposed that colchicine-induced diploid mutants arise from the substitution of chromosomes of similar phylogenetic origin (analogous chromosomes), and that the substitutions have not been detected cytologically because there is a tendency for bivalent rather than multivalent

FIGS. 1–4. Progeny rows of sorghum line 'Experimental 3' and of three diploid mutants obtained from 'Experimental 3' after colchicine treatment. The yardstick indicates height. FIG. 1. 'Experimental 3'. FIG. 2. True-breeding mutant. Class IV (Franzke & Sanders, in press). FIG. 3. True-breeding mutant. Class VB (Franzke & Sanders, in press). FIG. 4. Nontrue-breeding mutant; leaf width, head type, height, and maturity can be seen to segregate. Height differences are indicated by the bags which cover the main heads. Maturity differences are indicated by late unbagged plants, i.e., the first in the row, and early plants with well developed tillers which account for many of the unbagged heads.

pairing to occur in sorghums with $2n = 20$, and because pairing may occur between analogous chromosomes. Information from the literature, as well as research on the mutants, lends support to this view.

## Major Chromosome Changes

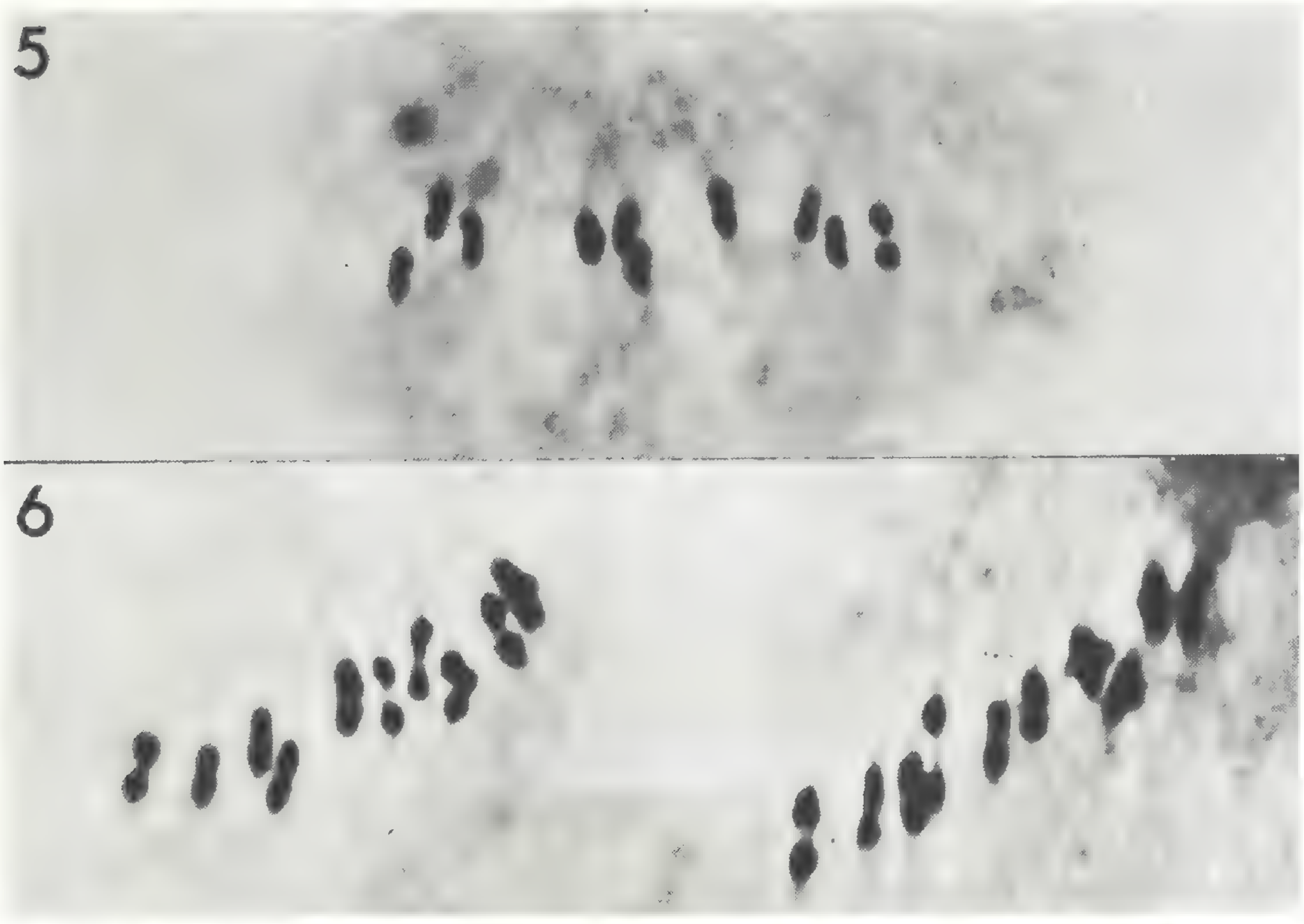
The phenotypic changes in the colchicine-induced diploid mutants appear to come about through major chromosome rearrangements since a large number of qualitative and quantitative characters are involved. Moreover, they are similar to natural variations found in sorghum varieties, and they include types which recur.

Similarly, complex mutants in other species have been shown to result from the addition or loss of entire chromosomes, i.e., in *Datura stramonium* L. (Blakeslee & Belling, 1924) and in *Lycopersicon esculentum* Mill. (Rick & Barton, 1954). In these species, the same complex mutants recurred and were shown to result from the addition or loss of the same chromosomes, either original chromosomes as in primary trisomics or monosomics, or isochromosomes as in secondary trisomics. Vasek (1956) working with *Clarkia unguiculata* Lindl., a highly variable outcrossed species, concluded that aneuploid types probably have characteristic phenotypes only in highly homozygous diploid species. Otherwise effects of aberrant chromosomes may be either obscured by variability among the diploid plants, as in *Zea Mays* L. (McClintock, 1929), or overshadowed by the effects of duplicated genes in various genomes, as in hexaploid *Triticum aestivum* L. (Sears, 1944, as *T. vulgare* Vill.).

Plants with extra chromosomes have been found in *Sorghum* (Endrizzi & Morgan, 1955; Hadley & Mahan, 1956; Price & Ross, 1957), but not in sufficient numbers in the same true-breeding line to establish whether or not the presence of a particular extra chromosome produces a particular phenotype. Since 'Experimental 3' is true-breeding and has a chromosome number of $2n = 20$, chromosome mutants in this line might be expected to be phenotypically distinct. If the distinct mutant complexes depend on the distribution of whole chromosomes, they would be likely to recur since the haploid chromosome number in *S. vulgare*, ten, is relatively small.

## Substitution of Whole Chromosomes

The mechanism for chromosome changes would have to be substitution since there is no change in chromosome number in the mutants. However, since substitution has not been detected cytologically, there would have to be additional factors which prevent the expected changes in chromosome pairing relationships. More detailed studies may reveal direct cytological evidence for chromosome substitution. Irregularities in the structure of some bivalents at metaphase in a nontrue-breeding mutant (FIGS. 5 and 6) were originally disregarded as possible artifacts. However, their repetition from cell to cell suggests that the ten bivalents in the mutant may not be the same ten bivalents as in 'Experimental 3'. It should be possible to interpret such apparent differences by studying earlier meiotic stages.




FIGS. 5, 6. Sorghum chromosomes at metaphase I in pollen mother cells. FIG. 5. 'Experimental 3'. FIG. 6. Nontrue-breeding mutant G (Sanders *et al.*, 1962). Cells of the mutant have two relatively large irregular bivalents in addition to a large bivalent similar to the one in 'Experimental 3'.

## Three Requisite Assumptions

ANALOGOUS CHROMOSOMES. The assumption that the haploid number of ten in *Sorghum vulgare* includes analogous chromosomes which can be substituted one for another without leading to inviability of the plant is basic. This assumption seems warranted as species of *Sorghum* with a haploid number of five are known, although not in the subgenus *Sorghum* [3] which includes *S. vulgare*.

Several investigators have concluded that the 20-chromosome diploid sorghums are of polyploid origin. Huskins and Smith (1934) based their conclusion primarily on the sporadic multivalents found in all species with $2n = 20$ studied, and on the frequent formation of multivalents in an asynaptic form of 'Dakota Amber Sorgo' in which normal pairing relationships were disrupted. Garber (1950) and Celarier (1958a), after examining the cytotaxonomic characteristics of the species of *Sorghum*, concluded that the "Eu-sorghums" are allopolyploids, i.e., *S. vulgare* with $2n = 20$ is an allotetraploid. Damon (1962) also considered that cultivated sorghums with $2n = 20$ are allotetraploids and suggested that if they have two genomes with slight homologies between corresponding chromosome pairs, the "secondary associations" frequently reported for *Sorghum* chromosomes could account for the inheritance of blocks of

[3] This subgenus should be called *Sorghum* rather than *Eu-sorghum* since it includes the type species (Art. 22, Int. Code Bot. Nomencl. 1961).

morphological characters frequently found following hybridization. He further pointed out that although Venkateswarlu and Reddi (1956) in their study of pachytene chromosomes of *Sorghum vulgare* var. *subglabrescens* (as *S. subglabrescens* (Steud.) Schwein. & Aschers.) identified ten distinct chromosome types, it seems feasible from their figures to arrange them as five pairs, the members of each pair differing primarily in arm length. A study of the paper itself reveals that, disregarding arm length, the chromosomes can be matched fairly well on the basis of the morphology of the heavily staining regions on either side of each centromere. The chromosomes have been numbered from 1 to 10 in order of decreasing length. The most probable pairs would appear to be: 1 and 3, 4 and 5, 2 and 9, 6 and 8, 7 and 10.

Allotetraploids are generally described in terms of separate genomes, designated A and B, in which corresponding chromosomes (1A, 1B; 2A, 2B; etc.) are those of similar phylogenetic derivation, hence those with the greatest degree of homology. Huskins (1931) suggested that such chromosomes "might be referred to as *homoeologous* chromosomes, signifying similarity but not identity" as in the case of *homologous*. Because of the confusion occasioned by the similarity of the two words, we have discarded *homoeologous* in favor of *analogous* to designate phylogenetically similar chromosomes.

The above indications of analogies among the ten haploid chromosomes of species of the subg. *Sorghum* are compatible with cytological studies which have been made on haploid plants of *S. vulgare*, including a haploid of line 'Experimental 3'. All investigators agree that occasional bivalents are found at late diakinesis and metaphase I of meiosis in pollen mother cells (Brown, 1943; Kidd, 1952; Endrizzi & Morgan, 1955; Sanders & Franzke, 1963). Rare associations of three or four have also been reported (Kidd, 1952; Sanders & Franzke, 1963). Endrizzi and Morgan (1955) considered that a reciprocal translocation and other abnormalities in progeny plants obtained by pollinating a haploid with a diploid of the same line resulted from crossing over in duplicate segments of partially homologous chromosomes, thereby providing evidence for the reality of pairing observed between chromosomes of the haploid.

Preliminary observations of pachytene chromosomes of sorghum haploids suggest that there are more paired than unpaired regions (Brown, 1943; Sanders & Franzke, 1963), and in haploid 'Experimental 3', cells at early diakinesis generally showed a multiple association including 5.5 chromosomes on the average. In some cells, all ten chromosomes were associated in a single complex in which most chromosomes were associated with at least two other chromosomes, some with more. The configuration seen in an individual cell appeared to depend on where separations had occurred in the complex. Cells at mid-diakinesis showed an average of 4.3 univalents and 2.1 bivalents with the remainder still in multiple associations. The large number of bivalents at this stage, in some cells four and very rarely five, suggests that some of the associations in the complex are more persistent than others and may indicate analogous chromosomes. The

occasional associations seen at late diakinesis and metaphase I may result from crossovers between like segments in analogous chromosomes, and the univalents may result from lack of crossovers due to the complexity of pairing relationships rather than from lack of pairing (Sanders & Franzke, 1963). These relationships between the chromosomes of an 'Experimental 3' haploid suggest that analogous chromosomes may differ by more than one translocation and agree with the interpretation suggested above for the work of Venkateswarlu and Reddi.

PAIRING OF ANALOGUES AND BIVALENT PAIRING MECHANISM. Analogous chromosomes in *Sorghum vulgare* would have to be sufficiently alike to pair under certain circumstances, and control of chromosome pairing would have to include a mechanism which promotes bivalent and limits multivalent pairing at the diploid level. These two assumptions are considered jointly because of interrelationships between them. Pairing of analogues is referred to by Waddington (1939, Chap. 2) and Stebbins (1947) as *heterogenetic association*. It is contrasted with *homogenetic association* (pairing of homologous chromosomes from the same genome), and is defined by Waddington as pairing between "homologous" chromosomes from different genomes when there is a considerable difference between them.

The most direct evidence for pairing of analogous chromosomes in *Sorghum* is furnished by the data on haploid plants cited above. Evidence that normal pairing is under genetic control is furnished by cases in which gene mutations have resulted in abnormalities. A spontaneous asynaptic mutation in 'Experimental 3' appeared to be a Mendelian recessive in relation to the normal (Ross *et al.*, 1960), and Huskins and Smith (1934) found an asynaptic strain of 'Dakota Amber Sorgo'. Examination of pairing relationships in sorghums with different chromosome complements gives some indication that a bivalent pairing mechanism may operate at certain chromosome levels in *Sorghum* and suppress formation of multivalents in some instances where they would otherwise be expected.

The degree of pairing in *Sorghum* would appear to depend on some sort of genetic balance which shifts with the genomes present. No evidence has appeared for localized control as in hexaploid *Triticum aestivum* where the presence of the long arm of chromosome V maintains bivalent pairing apparently without regard for the rest of the genotype (Riley *et al.*, 1960). However, there are correspondences between certain wheat plants lacking chromosome V and certain sorghum plants. In both species, pairing between analogous chromosomes occurs in haploids (Riley *et al.*, 1960; Sanders & Franzke, 1963) and in hybrids between species with different numbers of genomes, i.e., *T. aestivum* ($2n = 42$) $\times$ *Secale cereale* L. ($2n = 14$) (Riley *et al.*, 1960), and *Sorghum vulgare* ($2n = 20$) $\times$ *S. halepense* (L.) Pers. ($2n = 40$) (Hadley, 1953; Endrizzi, 1957). Some multivalent pairing occurs in *S. halepense*, but not enough to account for the degree of multivalent pairing in the hybrid (Celarier, 1958b). Addition of

chromosome V to the wheat plants eliminates analogous pairing, but controlling factors in *Sorghum* are not known.

Cytological studies of extra-chromosomal types at the diploid level in *Sorghum vulgare* have shown that the extra chromosomes occur more frequently as univalents than in multivalent configurations. For a trisomic derivative from a haploid, Endrizzi and Morgan (1955) reported 53 pollen mother cells with ten bivalents and a univalent, 19 with nine bivalents and a trivalent, and one with nine bivalents and three univalents. Extra-chromosomal types studied by Price and Ross (1957) were derived from an unknown triploid which they believed to be *S. vulgare* rather than a species hybrid. In 17 singly trisomic plants, ten bivalents and a univalent were found more frequently than nine bivalents and a trivalent at diakinesis and metaphase I; in three plants with two extra chromosomes, ten bivalents and two univalents were usually found; and in a fourth plant with two extra chromosomes, eleven bivalents were usually found.

Studies of multiple trisomics with from one to seven extra chromosomes in *Clarkia unguiculata* ($2n = 18$) showed an increase in trivalent formation with an increase in extra chromosomes. Trivalents per cell per extra chromosome were 0.43 for $2n + 1$, 0.46 for $2n + 3$, 0.56 for $2n + 4$, and 0.61 for $3n$ (Vasek, 1963). These results suggest that multivalent pairing may be influenced by a genetic balance which, in this case, shifts trivalent formation toward the frequency found in triploids when four or more extra chromosomes are present. Similar studies are needed in *Sorghum*.

Sorghums with a complement of 30 chromosomes have shown a high degree of trivalent formation whether $3n$ *S. vulgare* (Kidd, 1952), an unknown triploid (Price & Ross, 1957), or a hybrid between *S. vulgare* and either *S. halepense* or *S. almum* Parodi ($2n = 40$) (Hadley, 1953; Endrizzi, 1957). The number of trivalents per cell was highest for *S. vulgare* and *S. vulgare* × *S. almum* (from 8.2 to 8.5), and lowest for *S. vulgare* × *S. halepense* (from 5.7 to 5.8). Trivalent formation was consistently higher than the sum of trivalents and quadrivalents in corresponding 40-chromosome plants. Multivalent formation appears to be distinctly favored at the 30-chromosome level.

Cytological studies on tetraploids of *Sorghum vulgare* have shown a majority of the chromosomes associated as bivalents. In tetraploid *S. vulgare* var. *caffrorum* (Retz.) Hubb. & Rehd. (as var. *hegari* without authority, Chin, 1946), only three quadrivalents occurred per cell on the average and trivalents and univalents were rare. (Even the octoploid of the same variety had almost half the chromosomes in bivalent configurations.) In a tetraploid 'Experimental 3' plant, means of 3.3 quadrivalents, 0.04 trivalents, 12.8 bivalents and 1.2 univalents per cell were found (Sanders & Franzke, 1962b). Although multivalents are present uniformly in sorghum tetraploids, their formation is distinctly lower than in triploids, in spite of the increase in the number of homologous chromosomes.

These cytological data suggest several generalities concerning pairing relationships in *Sorghum* which need to be investigated. (1) Pairing of

analogous chromosomes may be limited chiefly to cases where a homologue is missing. Such a phenomenon could be designated as preferential pairing, the term used by Endrizzi (1957) to describe pairing relationships in *S. halepense*. (2) The tendency for bivalent pairing may be positively correlated with the presence of an even number of genomes, i.e., diploids and tetraploids. Configurations in *S. vulgare* haploids would have little bearing on bivalent or multivalent pairing as multiple associations appear to result from translocation differences between analogues. However, in triploids, trivalents are the rule. These relationships suggest that the bivalent pairing mechanism may be associated with genetic balance in some way. (3) Chromosome associations still present at diakinesis and metaphase I probably indicate only paired regions where crossovers occurred. Actual pairing relationships need to be studied at pachytene and diplotene.

## Patterns of Chromosome Substitution

Based on the above assumptions, different patterns of chromosome substitution may be considered, and their results predicted.

INDIVIDUAL CHROMOSOMES. If a single chromosome were lost and replaced by its analogue, the chromosome number would be unchanged, and, with analogous pairing and a tendency for bivalent formation, ten bivalents would be seen at diakinesis and metaphase I. Such a plant could be either phenotypically mutant or unchanged depending on the shift in genetic balance effected by the chromosomes involved. The self-progeny would segregate to a greater or lesser degree in direct proportion to the amount of crossing over which occurred between the paired analogous chromosomes. If more than one individual chromosome were lost and replaced by its analogue, the chances of the plant being phenotypically mutant would be increased, and the degree of segregation in the self-progeny would be increased. Such plants would be diploid nontrue-breeding mutants and would segregate for many characters.

PAIRS OF CHROMOSOMES. If a pair of homologous chromosomes were lost and replaced by their analogues, the chromosome number would be unchanged, and ten bivalents would be seen at diakinesis and metaphase I. Such a plant would be phenotypically mutant and would produce a uniform self-progeny of the same mutant type. Replacement of more than one pair of homologous chromosomes by their analogues would increase the number of such types which could be obtained. Such plants would be diploid true-breeding mutants changed for fixed complexes of characters.

INDIVIDUAL AND PAIRED CHROMOSOMES. If both single chromosomes and pairs of homologous chromosomes were lost and replaced by their respective analogues, the chromosome number would be unchanged, and ten bivalents would be seen at diakinesis and metaphase I. Such a plant would

be phenotypically mutant and would produce a self-progeny which would be uniform for some characters present in the parent mutant and segregate for others. Substitution of different numbers of individual chromosomes and pairs of chromosomes would produce intermediate diploid mutants ranging from those which would produce self-progenies primarily segregating, to those which would produce self-progenies uniform for many mutant characters.

## EVALUATION OF THE HYPOTHESIS

### Relevant Effects of Colchicine

That chromosomes may be lost and gained other than as entire genomes in cells of colchicine-treated tissues is indicated by the aneuploid types which have been obtained following colchicine treatment. In addition to polyploid types (some with aneuploid numbers) obtained from colchicine-treated *Datura* seeds, Bergner, Avery, and Blakeslee (1940) found $2n - 1$ plants at about 70 times the rate, and $2n + 1$ plants at about three times the rate that they were obtained from untreated seeds. Smith (1943) obtained aneuploids following colchicine treatment of two *Nicotiana* species and their $F_1$ hybrids. Both at diploid and polyploid levels, more of these plants resulted from chromosome deficiencies than from additions. One plant with the actual tetraploid number of 36 was off-type and appeared to have lost some chromosomes and gained others. The effects of colchicine on dividing cells can account for such phenomena.

ARRESTED MITOSES. The primary observable cytological effects of colchicine result from the inactivation of the spindle mechanism in dividing cells (Levan, 1938; Eigsti & Dustin, 1955, Chap. 2). Mitoses are interrupted at metaphase, and, after a delay, chromosome divisions may occur without nuclear or cell division so that doubled or polyploid numbers of chromosomes may be built up within a single nucleus and cell. During recovery, processes which take place in dividing cells frequently resume more or less out-of-phase with one another and result in abnormalities other than polyploid nuclei. Arrested metaphases assume various patterns from a single clump with centromeres congregated at the center and chromosome arms extended, to an "exploded" type with chromosomes scattered throughout the cell. Multiple clumps and multipolar spindles are common also so that, when followed by subdivision of the cell, polyploid chromosome groups may be reduced to smaller ones (Eigsti & Dustin, 1955, Chap. 2).

Delay in the division of the centromere accompanies inactivation of the spindle and results in characteristic "c-pairs" in which the daughter chromosomes remain attached only at the centromeres (Levan, 1938). After division of the centromeres, daughter chromosomes continue to lie parallel to one another and may remain so through several chromosome divisions so that an accumulation of the same chromosome is built up in

one position. Division of the centromeres is not simultaneous for all the "c-pairs" in one nucleus. There appears to be ample opportunity for two daughter chromosomes to act either as a unit or as two individuals during the irregularities of "c-mitoses" thereby making substitution of chromosomes by homologous pairs as plausible as by single chromosomes. True-breeding, nontrue-breeding and intermediate mutants would all be expected.

The suggestion of Bergner *et al.* (1940), that colchicine-induced delay of mitosis may exaggerate irregularities such as lagging and nondisjunction which in nature occur occasionally, should also be considered.

REDUCTION OF CHROMOSOMES IN SOMATIC TISSUES. As indicated above, multiple clumps and multipolar spindles in cells undergoing "c-mitoses" provide mechanisms whereby chromosome numbers may be reduced as well as duplicated during colchicine treatment.

Reduction of chromosomes in somatic tissues and its concomitant effects need further investigation. Isolated reports of chromosome reduction divisions and of haploid cells in somatic tissues led to a study of the phenomenon by Huskins (1948) and his associates. Colchicine was found to induce reductional groupings of chromosomes in root tips of *Tradescantia* and *Allium* (Allen *et al.*, 1950), and of *Sorghum* including line 'Experimental 3' (Atkinson *et al.*, 1957). The concept of somatic reduction has been part of explanations offered for the origin of colchicine-induced mutants from the beginning (Franzke & Ross, 1952). Although haploid plants have been obtained from colchicine-treated diploid seedlings, they have been extremely rare, if anything less frequent than from untreated seedlings. In one progeny-test plot, haploids occurred at the rate of approximately one per 1156 diploid plants. They were about seven times more frequent in progenies of untreated than of treated parents; the latter progenies were untreated plants a generation removed from colchicine treatment. On the other hand, following colchicine treatment of tetraploid 'Experimental 3' seedlings, four out of nine surviving plants were diploid and mutant (Sanders & Franzke, 1962b). A fifth plant was mixoploid and mutant. Phenotypic examination of 42 untreated plants from the same seed source and cytological examination of 37 of these indicated that all were still tetraploid and apparently unchanged. The diploid mutants obtained from tetraploids demonstrate that cells derived from reduction divisions in colchicine-treated tissues may survive and function in the production of new shoot apices. Reduction appears to take place more readily following treatment of tetraploids than of diploids, suggesting that reduction may occur more frequently in polyploid cells than at lower levels.

It is suggested that duplication provides the extra chromosomes necessary for substitution and, perhaps, an unbalance which favors reduction in somatic cells, and that reduction effects the return to the diploid level and the simultaneous redistribution of the chromosomes. Both loss and gain of chromosomes are consistent with these known effects of colchicine.

Substitution of analogous chromosomes in colchicine-induced mutants in *Sorghum* could be attributed to selection among the cells of the treated growing point which allows only viable and preferably vigorous chromosome combinations to continue to reproduce themselves and organize a meristem capable of giving rise to a mutant plant. Observations of Levan (1938) are in accord with such an assumption. He noted, in root tips of *Allium*, that diploid cells are favored over polyploid cells during recovery after colchicine treatment and are usually more numerous near the apex.

## Relevant Information on Colchicine-induced Mutants

The present explanation and the information that has been assembled on colchicine-induced mutants are generally in agreement. Several cases, however, remain controversial.

SIMILARITIES BETWEEN TRUE-BREEDING AND NONTRUE-BREEDING MUTANTS. There is no distinct separation between true-breeding and nontrue-breeding mutants since intermediate types appear which are true-breeding for some characters but not for others. All types may arise under the same conditions and in conjunction with one another (Sanders *et al.*, 1962). Such similarities suggest that all the diploid colchicine-induced mutants arise as variations of a single phenomenon. The present explanation accounts for all of the mutants as originating from different patterns of chromosome substitution.

"REACTOR" AND "NONREACTOR" LINES. That sorghum lines differ in their response to colchicine has been demonstrated in a comparison between the two lines 'Experimental 3' and 'Norghum' (Atkinson *et al.*, 1957). Lines such as 'Experimental 3' that produce a relatively high proportion of obvious diploid mutants following treatment have been termed "reactors," whereas those which produce only polyploids and minor variations have been termed "nonreactors." According to the present explanation, a line could give rise to such mutants if its chromosome complement included analogous pairs which could be substituted without impairing plant viability, and if the analogues were sufficiently different that substitution of one or both members of the pair resulted in obvious phenotypic changes. Such lines would have the fixed heterozygosity postulated by Huskins and Smith (1934) for sorghums with $2n = 20$ and would be "reactors." On the other hand, if a line had analogous pairs which could not be substituted without impairing plant viability, or if the analogues were not sufficiently different for substitution to result in obvious phenotypic changes, or if four homologues were present instead of two pairs of analogues in the five basic chromosome units, a line could not give rise to composite mutants by chromosome substitution and would be a "nonreactor." The many different types of sorghums have been so intermingled by hybridization that possible combinations of chromosomes from different sources would appear to be exceedingly large. Further, if pairing of

analogues occurs in certain hybrids and is accompanied by crossing over, new chromosomes unlike any of the originals would have been formed.

MUTANT INTERRELATIONSHIPS. Following colchicine treatment of one of the three Class I mutant lines shown to be genotypically as well as phenotypically alike (Chen *et al.*, 1961), four mutants were obtained which belong to three other classes of true-breeding mutants derived directly from 'Experimental 3' (Franzke & Sanders, in press). Also two true-breeding plants of the same type in an $F_1$ self-progeny from a nontrue-breeding mutant belong to a class derived directly from 'Experimental 3'. These results are consistent with the present explanation since a true-breeding or nontrue-breeding mutant derived directly from 'Experimental 3' could give rise to another true-breeding mutant type if chromosome substitutions which had taken place in the formation of the former did not preclude the substitutions necessary for the formation of the latter. If crossing over occurred between paired analogues in a nontrue-breeding mutant, chromosomes unlike any of the originals would be formed, and the probability of the self-progeny including types also derived directly from 'Experimental 3' would be decreased.

SEGREGATING PROGENIES FROM PHENOTYPICALLY UNCHANGED PLANTS. All true-breeding mutants and the majority of nontrue-breeding mutants have been recognized by phenotypic changes in the treated plants. However, some nontrue-breeding mutants have not been recognized until their self-progenies were grown. In some of these progenies there has appeared to be less segregation than in segregating progenies of recognized mutants (Sanders *et al.*, 1959), but this has not always been the case, i.e., mutant E (Sanders *et al.*, 1962). According to the present explanation, apparently unchanged treated plants could produce segregating self-progenies if only substitutions of individual chromosomes had occurred so that at least one of each of the ten haploid 'Experimental 3' chromosomes were still present, and if none of the substitutions shifted the gene balance sufficiently to be detected phenotypically.

APPARENT MUTATIONS OF SINGLE LOCI FROM DOMINANT TO RECESSIVE ALLELES. Genetic analyses of both true-breeding and nontrue-breeding mutants have provided instances of apparent single-gene changes, homozygous in the former and heterozygous in the latter (Foster *et al.*, 1961; Sanders *et al.*, 1962). Mendelian ratios for several qualitative characters were obtained in $F_2$ populations from crosses between true-breeding mutants and the parent line 'Experimental 3', and in first generation self-progenies of nontrue-breeding mutants. Except where the mutants were intermediate, having both nontrue-breeding and true-breeding mutant characters, nontrue-breeding mutants behaved genetically much like $F_1$ hybrids between true-breeding mutants and 'Experimental 3'. According to the present explanation, strictly nontrue-breeding mutants would be equivalent to such $F_1$ plants.

If 'Experimental 3' is a fixed heterozygote for many genes as the result of an allopolyploid origin at the same time it is a true-breeding line, then the dominant alleles for these genes would be present on both homologues of one chromosome pair and the recessive alleles would be present on both members of the analogous pair. If the pair carrying the dominant alleles were replaced by an additional pair carrying the recessive alleles, the recessive phenotype would appear in the mutant and all its progeny. If such a mutant were crossed with 'Experimental 3', the $F_1$ would contain three homologous chromosomes carrying the recessive allele and one analogue with the dominant allele, and would exhibit the dominant phenotype. With analogous and bivalent pairing, a 3:1 ratio for dominant: recessive phenotype would be obtained in the $F_2$ population. If an individual chromosome of 'Experimental 3' carrying a dominant allele were replaced by an additional chromosome carrying the recessive allele, the nontrue-breeding mutant would be genetically equivalent to the above $F_1$ plant for that particular unit of four chromosomes. It would seem that apparent mutations from dominant to recessive alleles may result from chromosome substitution rather than from point mutation.

COMPLEX DIPLOID MUTANTS NOT INDUCED BY COLCHICINE. Diploid mutants have arisen without colchicine treatment in self-progenies both of unstable 'Experimental 3' polyploids (Franzke *et al.*, 1962) and of 'Experimental 3' plants homozygous for an asynaptic gene (unpublished). These findings are in agreement with the present explanation since mutants should result from any interruptions of normal chromosome behavior which could result in new combinations. Multivalent pairing in a polyploid and lack of normal pairing in an asynaptic plant would result in gametes containing chromosome groups other than the normal complement. Diploid mutants could result from viable combinations either in $2n$ egg cells which developed parthenogenetically, or in haploid egg cells or pollen grains which effected fertilization. As would be expected, the three mutants from the asynaptic line were nontrue-breeding. The two diploid mutants found in polyploid self-progenies were true-breeding. Yet progeny plants in both groups showed an excess of univalents during meiosis I.

CHROMOSOME IRREGULARITIES IN NONTRUE-BREEDING MUTANT PROGENIES. Although irregularities of chromosome behavior have not thus far been found in true-breeding or nontrue-breeding mutants obtained from colchicine-treated diploid seedlings, some abnormalities were found in plants from nontrue-breeding mutant progenies (Sanders & Franzke, 1962a). The principal abnormality was an increase over untreated plants in the number of univalents at diakinesis and metaphase I in pollen mother cells. Rare trivalents and quadrivalents were also found, but since several investigators have reported occasional multivalents in various diploid sorghum lines (Huskins & Smith, 1934; Chin, 1946; Hadley, 1953), these cannot necessarily be attributed to the mutant condition. The increase in univalents in these plants is in agreement with the present explanation

since the pairing of analogous chromosomes in nontrue-breeding mutants would be expected to result in some chromosome irregularities in the progeny plants, especially if crossing over had occurred and interchanged segments of the analogues. Irregularities in pairing relationships should be sought in nontrue-breeding mutants, $F_1$ hybrids between true-breeding mutants and their parent lines, and plants from nontrue-breeding self-progenies and from $F_2$ populations. Crossovers between analogues would be equivalent to translocations between these chromosomes, but the usual translocation configurations would not be expected if there is a bivalent pairing mechanism.

APPARENT MUTATIONS FROM RECESSIVE TO DOMINANT ALLELES. 'Experimental 3' exhibits the dominant phenotypes of the three observed characters which might be attributed to single-gene differences. These are red as opposed to green seedling-base, dry as opposed to juicy stalk and midrib, and awnless as opposed to awned spikelets (Quinby & Martin, 1954). A Class I mutant line which exhibits the recessive phenotypes for all three characters, when treated with colchicine, gave rise to mutant lines belonging to three other classes which included at least one apparent mutation from recessive to dominant for each of the characters (Franzke & Sanders, in press). According to the present explanation, the Class I mutant would have resulted from the replacement of pairs of homologous chromosomes carrying the dominant alleles by their analogues carrying the recessive alleles. No further substitution would be possible in these units of four chromosomes since they would now consist of four homologues, and a source for the return to the dominant phenotype is not evident.

However, sorghum genetics is not sufficiently understood to make a reliable interpretation of genotype on the basis of phenotypic observation alone. Similar phenotypes in sorghums have been found to result from different genotypes, alleles of certain genes have been found to have different phenotypes in different genetic constitutions, and gene interaction has been found to be common (Celarier, 1958a). Class I mutants have been analyzed genetically in relation to 'Experimental 3' and to each other (Chen *et al.*, 1961). It would be necessary to analyze mutant lines from the classes obtained both from Class I and from 'Experimental 3' in relation to both parental lines before any conclusions could be drawn.

In other species, characters identified with particular genes have been found to change phenotypically in chromosome mutants without the chromosome carrying the known gene being involved, i.e., in *Datura* (Blakeslee, 1922) and in tomato (Lesley, 1928). Rick and Barton (1954) noted little or no relationship between the phenotype of a trisomic in tomato and the genes known to be on the extra chromosome. Such results indicate the complexity of phenotypic effects brought about by chromosome changes and suggest that apparent changes from recessive to dominant phenotypes might come about through chromosome substitution.

CHROMOSOME PAIRING RELATIONSHIPS IN COLCHICINE-INDUCED DIPLOID MUTANTS. Because of the presence of ten bivalent chromosomes at diakinesis and metaphase I of meiosis in pollen mother cells of colchicine-induced diploid mutants and their $F_1$ hybrids with other sorghum lines, the present explanation depends on analogous pairing and on a mechanism for bivalent pairing in diploid sorghums with 20 chromosomes. As cited above, instances of analogous pairing in *Sorghum* are known. The bivalent pairing mechanism provides the greatest difficulty since, as presented earlier, multivalents are found in *Sorghum*: in tetraploids, especially in triploids, sometimes in trisomics at the diploid level although a bivalent and a univalent are more usual, and very occasionally in straight diploids where they would seem to involve analogous pairing. It is on the basis of the rarity of multivalents in diploids and their relative infrequency in trisomics that it is proposed that bivalent pairing may be the rule and multivalent pairing the exception at the 20-chromosome level. Following a polyploid origin, the sorghums with $2n = 20$ may have undergone "diploidization" which included the establishment of bivalent pairing even though the analogous chromosomes retain the ability to pair with one another, especially when uneven numbers of homologues are present. However, a clearcut understanding of the control of bivalent pairing, such as that worked out for hexaploid wheat, is needed.

## IMPLICATIONS OF THE HYPOTHESIS FOR THEORETICAL AND APPLIED RESEARCH

If colchicine-induced diploid mutants in *Sorghum* result from substitution of analogous chromosomes, it should be possible to obtain the same results with other plants of allopolyploid derivation in which analogous chromosomes are sufficiently similar that they can be interchanged without an adverse effect on plant viability. If such mutants were to be easily recognizable, it would be necessary that the analogous chromosomes carry different alleles which would result in distinct phenotypes, and that the original line be true-breeding and preferably not too highly polyploid so that changes would not be obscured by the variation in the original population, or covered by the multiple effects of alleles of the same genes on other chromosomes. In *Linum usitatissimum* L., colchicine treatment of seedlings heterozygous for known genes resulted in one plant with branches homozygous for the gene markers (Dirks *et al.*, 1956). Homologous chromosomes carrying different alleles may have been substituted for one another. Since this species ($2n = 30$) is thought to be of polyploid and perhaps of hybrid origin (Ray, 1944), it might also be expected to produce diploid mutants following treatment of seedlings of true-breeding lines. Meanwhile, the results suggest that, in heterozygous plants not necessarily of allopolyploid origin, it may be possible to induce substitution of homologous chromosomes for one another by colchicine treatment, and hence to obtain homozygosity from heterozygosity without generations of inbreeding.

As stated earlier, there is some evidence that diploid mutants are obtained under conditions of colchicine treatment more stringent than those required to produce polyploids. Success in obtaining mutants depends on the skill of the researcher in insuring survival of treated seedlings under adverse circumstances. Environmental factors favorable for the production of mutants probably vary with the material, but if conditions necessary to obtain polyploids with colchicine are known, they could be taken as the starting point from which to develop more rigorous methods of treatment while still keeping the plants alive. Treated seedlings under favorable growing conditions appear to outgrow the effects of colchicine (Sanders *et al.*, 1959). It would seem necessary to delay growth long enough to allow the drug not only to act (duplication of chromosomes to produce polyploid cells), but also to react (subdivision of polyploid cells to produce cells with viable new diploid complements) while still keeping the material alive. To what extent mutants can be obtained by colchicine treatment of plants other than *Sorghum* needs to be determined.

In either a research or a breeding program, colchicine treatment would provide a method for obtaining recombinations of substitutable chromosomes, sometimes accompanied by homozygosity, within the genetic complement either of an established line or of a hybrid. The method has been used in the sorghum-breeding program at South Dakota State College, and new true-breeding lines have been obtained and released as agronomic varieties following treatment both of seedlings from true-breeding lines, i.e., 'Winner' (Class II, Franzke & Sanders, in press), and of hybrid seedlings, i.e., 'Dual' (Franzke, 1958). If substitution of individual chromosomes does occur, crossing over between paired segments of analogous chromosomes could result in recombination of parts of chromosomes as well as of whole chromosomes in the progeny.

If the hypothesis is correct, the method in use in the sorghum program is basically similar to the new approach to plant breeding described by Riley (1963) for wheat. New possibilities are opening up following the discovery that elimination of chromosome V removes the limitations imposed by bivalent pairing and permits recombinations of chromosomes and chromosome segments between genomes. He writes, "In wheat we now have the first example of a system by which recombination between different parental patterns can be modified. The impact of this notion on plant breeding as a whole has still to be determined, but it could be considerable." It may prove possible to obtain recombinations between different genomes in a plant by using colchicine to bring about chromosome substitutions in somatic tissues, thus bypassing established bivalent pairing mechanisms. Use of asynaptic plants to interchange chromosomes between genomes should also be investigated.

The degree of variability which might be obtained by using the method would depend on the genetic constitution of the original material. Treatment of a polyploid line which is a fixed heterozygote for many genes should provide a limited example of Stebbins' (1940) description of possibilities for evolution within a polyploid complex: "It can produce

endless new species, but these are all or nearly all new combinations of the same supply of genic material; they are new variations on an old theme."

## SUMMARY

An hypothesis is presented that explains the diploid mutants which arise in certain lines of *Sorghum* following colchicine treatment of seedlings as resulting from the substitution of analogous chromosomes originally present in the genetic constitution of sorghums with $2n = 20$.

Nontrue-breeding mutants are formed if there are substitutions only of individual chromosomes; true-breeding mutants, if there are substitutions only of pairs of homologous chromosomes; intermediate mutants, if there are substitutions of both individual chromosomes and pairs.

These chromosome substitutions are not detected at diakinesis or metaphase I since no abnormal pairing configurations result. Pachytene and diplotene chromosomes in nontrue-breeding mutants and in $F_1$ hybrids involving true-breeding mutant lines need to be carefully examined for evidence of analogous pairing.

*Sorghum* and other species, particularly those of polyploid and hybrid origin, need to be investigated intensively in order to establish whether this hypothesis concerning colchicine-induced chromosome substitution is valid.

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# STUDIES IN ALYSSUM: NEAR EASTERN REPRESENTATIVES AND THEIR ALLIES, I

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In the course of a monographic study * of the genus *Alyssum* L., a number of previously undescribed taxa from Turkey were discovered. In this paper these are described, and new combinations, also resulting from the study, are made. In addition, the new species are assigned to the appropriate section, subsection, or series, several of which are new to the nomenclatural hierarchy of *Alyssum*. In an earlier paper (Dudley, 1962), a few new taxa from the Near East with extra-Turkish distributions were described and discussed. The corpus of the taxonomic treatise, to be published at a later date, will take into consideration generic limits within the Cruciferae, tribe Alysseae, provide keys for identification of species of *Alyssum*, and consider the systematics of the Near Eastern species and their allies.

The place names given in the most recent atlas of Turkey (Büyük Atlas, Duran: Istanbul, 1962) are utilized whenever necessary and possible. Occasionally, the names of the Roman Provinces in Anatolia have been used; a paper by Davis (1953) elucidates the boundaries of these provinces in relation to the current Provinces or Vilâyets. The phytogeographical areas in Turkey are exceedingly complex, and, for the most part, the terminology applied to them has been avoided; however, when used, the terms "Irano-Turanian," "Mediterranean," and "Euxine" are applied in the sense of Davis (1951).

The method of arranging specimen citations according to convenient grid squares (for Turkey) is based on an arbitrary division of land areas enclosed by 2° latitude and 2° longitude. For example, as seen on the map, Text-fig. 1, the land mass enclosed between 40°–42° latitude and 28°–26° longitude is given the grid epithet of A1. Unless otherwise stated, all specimens cited have been examined. The collections made by the author in 1962 are numbered in the sequence of the Davis Anatolian collections, i.e., *Dudley (D. 25680)* was collected by the author but numbered as a part of the Davis material. Exclamation points (!) are inserted directly following the synonym citations if the types or isotypes of these synonyms (or in the case of generic synonyms, the type material of the type species) have been seen. No exclamation point is appended if the type material of synonyms has not been seen, though such names are included only when there is no doubt regarding their identity.

The taxa described here as new are predominantly from the very

* In partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Edinburgh.

extensive Near Eastern collections made within the past twenty years by Dr. P. H. Davis and his co-collectors, and Dr. A. Huber-Morath. With the exception of *Alyssum corningii*, *A. harputicum*, *A. davisianum*, and *A. huber-morathii*, the other new species were brought to my attention by Dr. Huber-Morath, who recognized them among his own Anatolian collections as being undescribed. I am extremely grateful to Dr. Huber-Morath for putting his entire collection of *Alyssum* at my disposal, for his collaboration, and for his kind permission to publish the six new species which he discovered and for which he suggested the specific epithets. Without the cooperation of the directors of numerous herbaria, clarification of the taxonomic confusion within the genus *Alyssum* or definitive typification of taxa could not have been attempted. From the following herbaria approximately 1,500 specimens, including many types, were borrowed. In addition to the specimens which were received on loan, the author studied approximately 6,000 specimens in those herbaria that are preceded by an asterisk (*).

* Arnold Arboretum, Harvard University, Cambridge, Massachusetts, U.S.A. (A).
* Ankara Üniversitesi Fen Fakültesi Botanik Enstitüsü, Ankara, Turkey (ANK).
Universitetets Botaniske Museum, Bergen, Norway (BG).
* British Museum (Natural History), London, England (BM) (including the Clifford herbarium).
Slovenské Múzeum, Bratislava, Czechoslovakia (BRA).
* Royal Botanic Garden, Edinburgh, Scotland (E).
* Conservatoire et Jardin Botaniques, Genève, Switzerland (G) (Delessert herbarium, Barbey-Boissier herbarium, Edmund Boissier herbarium, B.V.D. Post herbarium, and the De Candolle herbarium).
* Gray Herbarium, Harvard University, Cambridge, Massachusetts, U.S.A. (GH).
* Private collection of Dr. A. Huber-Morath, Basel, Switzerland (HM).
Department of Botany, Hebrew University, Jerusalem, Israel (HUJ).
* Farmakobotanik ve Genetik Enstitüsü, Fen Fakültesi, Istanbul, Turkey (ISTF).
Institut für Spezielle Botanik und Herbarium Haussknecht, Jena, Germany (JE).
* Herbarium, Royal Botanic Gardens, Kew, England (K).
Botanical Institute of the Academy of Sciences of the Ukrainian S.S.R., Kiew, Russia (KW).
Rijksherbarium, Leiden, Netherlands (L).
Komarov Botanical Institute of the Academy of Sciences of the U.S.S.R., Leningrad, Russia (LE).
Hartley Botanical Laboratories, Liverpool, England (LIVU).
* The Linnean Society, London, England (LINN).
Instituto "Antonio José Cavanilles," Madrid, Spain (MA).
* The Fielding and Druce Herbarium, Department of Botany, Oxford, England (OXF).
Muséum National d'Histoire Naturelle, Paris, France (P).
Botanical Department of the National Museum, Praha, Czechoslovakia (PR).
Botanische Abteilung der Württenbergeschen Naturaliensammlung, Stuttgart, Germany (STU) (Anatolian collection of Kühne).
* Naturhistorisches Museum, Wien, Austria (W) (the General herbarium, the private collection of K. H. Rechinger, and the Hálácsy herbarium).

TEXT-FIG. 1. Map of Turkey, showing grid system used in citation of specimens. For explanation see text.

Botanisches Institut und Botanischer Garten der Universität, Wien, Austria (WU).
Botanischer Garten und Museum der Universität, Zurich, Switzerland (Z) (Anatolian collections of Markgraf).

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**Alyssum** Linnaeus, Sp. Pl. 2: 650. 1753; Gen. Pl. ed. 5. 293. 1754. LECTOTYPE SPECIES: *Alyssum montanum* L. (!) (See Britton & Brown, Ill. Fl. North. U.S. ed. 2. 2: 154. 1913; Hitchcock & Green, 1929).

*Meniocus* Desv. Jour. Bot. Appl. 3: 173. 1814. TYPE SPECIES: *Alyssum linifolium* Steph. ex Willd. (!).

*Ptilotrichum* Meyer in Ledebour, Fl. Alt. 3: 50. 1831. TYPE SPECIES: *Alyssum canescens* DC. Syst. Nat. 2: 322. 1821 (!). Lectotype, Russia. In rupestribus montosis Siberiae, Mt. Altai, 1819, *Fischer s.n.* (G–Herb. DC., as *A. sibiricum*).

*Psilonema* Meyer, *ibid.* LECTOTYPE SPECIES: *Alyssum dasycarpum* Steph. ex Willd. Linn. Sp. Pl. ed. 4. 3(1): 469. 1800 (!). Holotype, Russia. In Sibiria ad Kamam et Volgam fluvium, *Stephan* (LE, non vidi); isotypes (BM, G, K).

*Odontarrhena* Meyer, *ibid.* 58. LECTOTYPE SPECIES: *Alyssum tortuosum* Willd. (!).

*Gamosepalum* Hausskn. Mitt. Thür. Bot. Ver. 11: 73. 1897. LECTOTYPE SPECIES: *Gamosepalum lepidoto-stellatum* Hausskn. & Bornm. ex Hausskn. (!).

*Triplopetalum* Nyárády, Magyar Bot. Lap. 24: 97. 1925. TYPE SPECIES: *Triplopetalum pinifolium* Nyár. (!).

Section **Meniocus** (Desv.) Hook. in Benth. & Hook. Gen. Pl. 1: 74. 1862. TYPE SPECIES: *Alyssum linifolium* Steph. ex Willd. Linn. Sp. Pl. ed. 4. 3(1): 467. 1800 (!). Syntypes, Crimea and Caucasus.

Tauria et Armenia, *Stephan s.n.* (B, non vidi); isosyntype, "Tauria" (G).

**Alyssum blepharocarpum** Dudley & Huber-Morath, sp. nov. Holotype, Turkey, *Huber-Morath 13722* (HM); isotype (E). PL. I, FIGS. 1–13.

Affinis *A. huetii* Boiss. sed habitu diverso, fructibus minoribus, stylo longiore, petalis maioribus, glandulis globosis (haud subulatis) differt.

*Herba* annua, 7–15(–18) cm. alta et lata, e basi ramosa caulibus tenuibus erectis vel patentibus parce foliatis. *Planta* ex toto virescens vel cinereo-cana, saepe ad maturitatem rubro-purpurea, indumento pilis stellatis appressis minute punctatis brevibus ramosis 4–6 radiatis ut videtur multi-radiatis 0.2–0.4 mm. diametro vestita. *Folia* linearia, oblanceolata vel rare subspatulata, obtusa vel acuta, sessilia, vel ad basim sensim attenuata, (3.5–)8–20(–25) mm. longa, 0.5–2 mm. lata, summam versus decrescentia. *Inflorescentia* 5–12(–20) cm. alta et lata, simplex vel corymbosa, ramulis simplicibus ascendentibus 2.5–5(–8) cm. altis. *Pedicelli* 3.5 7.5 mm. longi, subhorizontales vel divergentes inter se 4–7 mm. distantes, pilis stellatis minutis appressis paucibus radiis inaequalibus parce vel copiose provisi. *Sepala* elliptico-ovata vel lanceolata, (1.5–)2.5–3 mm. longa, 0.8–1 mm. lata, margine hyalina angusta, pilis stellatis appressis parce vel copiose vestita, interdum dorsaliter carinata 1–5 pilis stellatis basi manifeste tuberculatis provisa. *Petala* in sicco flava vel subflava, obovata, retusa vel subretusa rare integra, in unguem brevem angustum sensim attenuata, glabra vel solum in ungue pilis stellatis provisa, (2.5–)3–4(–5.5) mm. longa, 1–2.5(–3.5) mm. lata. *Filamenta longa* (1.5–)2–3.5 mm. longa, bilateraliter alata; ala una quam altera latior, 1–3-denticulata, apice libero 0.5 mm. longo. *Filamenta brevia* 1.5–2.5 mm longa, appendice ad basim connato acuto vel minute 2–3-denticulato (0.5–)0.7–1(–1.5) mm. longo. *Glandulae* bene evolutae, globosae, lobatae. *Antherae* auriculatae, apice obtusae vel acutae, 0.5–0.6 mm. longae. *Stylus* glaber, rigidus, tenuis, (0.7–)1–1.5(–2) mm. longus, stigmate magno provisus. *Silicula* ovato-orbiculata vel elliptica, obtusa vel truncata, rare acuta vel emarginata, 3.5–4.5(–5) mm. longa, (2–)2.3–3.2(–3.8) mm. lata, semper setis tenuibus vel robustis antrorsis basi dilatatis ad marginem provisa, valvis membranaceis manifeste nervosis aequaliter compressis minute papillosis vel glabris vel setis eis ad marginem similibus copiose provisa. *Ovula* in placenta lateraliter inserta, 2 or 3 (4) per loculum. *Semina* brunnea, 1.5–2 mm. longa, 1–1.5 mm. lata, ala (0.1–)0.2–0.3 mm. lata. Fl. Apr.–July, fr. May–July.

DISTRIBUTION AND HABITAT: Anatolian endemic in disturbed situations, cultivated and neglected fields, *Astragalus* and salt steppe, gypsum outcrops and Tertiary rocks; alt. 500–1620 m.

**Turkey.** A3: Prov. Ankara, Ankara-Sariyar, Sakaryatal, 139 km. westlich Ankara auf Tertiärboden, 26 Apr. 1955, *Walter 1359* (HM); westlich Beypazari,

Yëniköy-Sakarya Strasse, Steppe, 500 m., 27 May 1957, *Kühne 267, 263a* (STU); Beypazari, Nähe Abzweigung nach Tepeköy, Feld, 1 June 1957, *Kühne 496* (STU); Uytepe, Gipfelgrat, Steppe, 7 June 1957, *Kühne 733, 726* (STU). A8: Prov. Gümüşane, dist. Bayburt, Gümüşane-Bayburt, Linsenfeld, 21 km. vor Bayburt mit *A. stylare*, 1620 m., 15 July 1958, *Huber-Morath 16485* (HM). B4: Prov. Konya, Cihanbeyli, steppe, fl. lutea, 7 June 1952, *Davis 18636* (BM, E, K); Prov. Ankara, dist. Kadinhan, Sarayönü-Cihanbeyli, Weizenfeldrand, 13 km. nordöstlich Sarayönü, 870 m., 1 June 1956, *Huber-Morath 13722* (HM, E); Angora (Ankara), Frichès a Kodja-dagh, 8 July 1908, *Frères E. C. 458* (E, G); Kavakli Dere, Steppe im Gelände der Deutschen Botschaft, Andesitlehm, 900 m., 30 May 1958, *Markgraf s.n.* (Z); Steppen-Probenfläche, 7 May 1958, *Markgraf s.n.* (Z); Bergsteppe, Hussein bei Ankara, 4 June 1932, *Kotte 171* (K); Wegrand am alten Flugplatz von Ankara, 850 m., 11 June 1949, *Huber-Morath 9317* (HM); dist. Şerefli Koçhisar, versalzte Steppe am Tuz gölü, 114 km. südlich Ankara, 11 km. südlich Sekerköy, 920 m., 26 June 1959, *Huber-Morath 16079* (HM); Ankara-Gölkarindan, soma yol Lenari, 20 June 1953, *Birand & Zohary 2928* (ANK). B7: Prov. Erzincan, Başköyukten, km. somas Ekim tarlan Lenari, 1020 m., 30 May 1956, *Birand 141* (ANK).

In central and eastern Anatolia, *Alyssum blepharocarpum* grows in small, scattered populations. It is closely related to *A. huetii* Boiss. with which it is broadly sympatric. It differs from the latter by being a more delicate and spreading plant, having smaller and often orbicular or ovate fruits with sparser setae (or none) on the valves, longer styles, larger petals, and globose lobed glands.

In the eastern part of its range *Alyssum blepharocarpum* is partially sympatric with *A. stylare* (Boiss. & Bal.) Boiss., which has its center of distribution farther south in the Cappadocian steppe and which may be distinguished from *A. blepharocarpum* by its longer styles, larger and bifid petals, and larger and elliptic fruits with longer, denser setae on the valves.

In sect. MENIOCUS, *Alyssum huetii, A. blepharocarpum, A. stylare,* and *A. heterotrichum* Boiss. possess simple stiff setae on their fruits, but *A. blepharocarpum* is the only species among these which has such a wide range of variation in fruit indumentum. When the specimens which are cited above were examined individually it appeared that three different combinations of indumentum types were present on the fruit (PL. I, FIGS. 2–5). These indumentum states are: 1) marginal setae 0.2–0.4 mm. long, the valve surfaces minutely papillose (*Davis 18636*); 2) marginal and surface setae 0.4–0.5 mm. long, the valve surfaces papillose or glabrous (*Huber-Morath 13722*); 3) marginal setae 0.2–0.4 mm. long, the valve surfaces always glabrous (*Huber-Morath 1359b*). It was soon evident when the gatherings were compared with one another that the indumentum on the fruit could not be employed to distinguish three distinct taxa. No geographical pattern emerged to correlate with the three indumentum states which sometimes occurred, not only on different plants from the same population, but also on different fruits of the same plant.

This new species was first pointed out to the author by Dr. A. Huber-Morath in his private herbarium in Basel, Switzerland; however, it was

first collected near Ankara in 1908 by *Frères des E. C.* (*No. 458*). The Latin and French descriptions which Aznavour attached to this collection were never published, and Dr. Huber-Morath suggested as appropriate the specific epithet *blepharocarpum* (Greek, *blepharis*, eye-lash), referring to the short setae on the fruit.

Section **Alyssum**. LECTOTYPE SPECIES: *Alyssum montanum* L. Sp. Pl. 2: 650. 1753 (!).

**Alyssum minus** (L.) Rothmaler, Repert. Sp. Nov. **50**: 77. 1941. — Breistroffer, Bull. Soc. Bot. Fr. **103** (82 Sess. Extra.): 153. 1956; Heywood, Repert. Sp. Nov. **64**: 54. 1961.

*Clypeola minor* L. Flora Monspeliensis (Nathhorst, Dissert. [no. 70] 21. 1756 — non *Amoenitates Academicae* 4. 1759). Type: Magnol, *Botanicum Monspeliensis* ed. 2. 251. 1688 — "Thlaspi Alysson dictum minus, capsulis majoribus rotundis, non foliatis."

*Alyssum campestre* L. Sp. Pl. ed. 2. **2**: 909. 1763, *pro parte — non* 1759(!). — Turrill, Jour. Bot. (Lond.) **73**: 261. 1935; Degen, Fl. Velebitica **2**: 187. 1937; Maire, Bull. Soc. Hist. Nat. Afr. Nord **30**: 258. 1939; Zohary, Palest. Jour. Bot. Jerusalem Series **2**: 161. 1941; Rechinger f. Ark. Bot. II. **2**: 345. 1953.

*Alyssum parviflorum* Bieb. Suppl. Fl. Taur. Cauc. **3**: 434. 1819(!). — Turrill, *loc. cit.*; Maire, *loc. cit.*

Frequently, botanists confuse *Alyssum minus* (L.) Rothmaler (= *A. campestre* auct.) with *A. alyssoides* (L.) L. in sect. PSILONEMA. In addition to the subulate, wingless, edentate and unappendaged filaments of the latter, *A. alyssoides* can be separated readily from *A. minus* by having sepals always persistent. The specific epithet, *alyssoides*, was furnished by Linnaeus in *Species Plantarum* (**2**: 652. 1753) under *Clypeola* No. 2, which he transferred to *Alyssum* in *Systema Naturae*, ed. 10. 1759. Most taxonomists today accept the binomial *A. alyssoides*, which is typified by a specimen extant in the Clifford herbarium (BM), though Linnaeus redescribed this specimen in the second edition of *Species Plantarum* (1763), as *A. calycinum*.

The crux of the problem concerning the application of the binomial *Alyssum minus* or *A. campestre* is the identity and typification of *Clypeola campestris* of *Species Plantarum* (1753). Though *Clypeola* No. 3, found on page 652 of *Species Plantarum*, is not furnished with a trivial epithet, the name *campestris* is found on page 1231 in the Errata. Linnaeus refers to Sauvage, *Methodus Foliorum Monspeliensis* . . . 71. 1751, which reads "No. 405 Clyp. annua siliculis bilocularibus dispermis calyce persistente. . . ." This Sauvage description must be regarded as the basis of *Clypeola campestris*. Though no specimens of *Alyssum* or *Clypeola* in the Linnaean herbarium are marked with an "M," indicating their origin from Sauvage (cf. Stearn, Introduction to *Species Plantarum*, facsimile, 1957; Savage, 1945), it is logical to assume that Sauvage's mention of

persistent sepals could apply only to *Alyssum alyssoides*, rather than to the other taxon commonly, but incorrectly, called *Alyssum campestre*, whose sepals are *always early deciduous*. That Linnaeus later altered Sauvage's circumscription in the second edition of *Species Plantarum* to read: ". . . calycibus caducis . . ." is not relevant to the problem of typifying *Clypeola campestris*, or as it later became, *Alyssum campestre* (*Systema Naturae*, ed. 10. 1759).

Further evidence is gathered from the C. Bauhin polynomial, "Alysson dictum campestre minus" (*Pinax*, 107. 1623) which is referred to indirectly by Sauvage through Tournefort (*Institutiones rei herbariae* 1: 217. 1700—"Alyss. incanum serpilli folio minus"), and directly by Magnol in *Botanicum Monspeliense*, 251 (ed. of 1688). This Bauhin polynomial is cited by Linnaeus in *Species Plantarum* (1753) as a synonym of *Clypeola campestris* and as a possible synonym of *Clypeola alyssoides* in *Hortus Cliffortianus* (329. 1738). Linnaeus in *Flora Monspeliensis* (Nathhorst, Dissert. [no. 70] 21. 1756.) refers *Clypeola campestris* to No. 1137 in Magnol's work. Linnaeus's own copy of this work (at the Linnean Society, London) is numbered in his handwriting, and No. 1137 falls on the entry (page 251) which reads: "Thlaspi dictum campestre minus . . . ."

Dr. M. Geiger-Huber, of the Botanisches Institut der Universität Basel, Switzerland, states (in a letter) that, although there are no authentic specimens of "Alysson dictum campestre minus" in the Bauhin Herbarium, C. Bauhin wrote in the *Catalogus Plantarum circa Basileam* . . . (1622) that it was common in the fields around Basel. As only two species of *Alyssum* are known to occur near Basel, the alpine *A. montanum*, and the common weed, *A. alyssoides*, it may be inferred that the Bauhin polynomial refers to the latter.

Rather than increase the nomenclatural confusion which would be implicit if the binomial *Alyssum campestre* were substituted for *A. alyssoides*, it is preferable to retain *A. alyssoides* for the taxon with *persistent sepals*, and treat *Alyssum campestre* as a synonym of it.

Now that it is clear that *Alyssum campestre* can be reduced to a synonym of *A. alyssoides*, the next unambiguous binomial must be found and applied to the plant which has long masqueraded as *Alyssum campestre* and which has *early deciduous sepals*.

Turrill (1935), who recognized the confusion implicit in the Linnaean *Alyssum campestre*, claimed that Linnaeus himself used the name in different senses and suggested that since this initial confusion has been a persistent source of error "*A. campestre*" should be rejected as a *nomen confusum*. He advocated the application of *A. parviflorum* Bieb. (1819), as did Maire in 1939. It is interesting to note that, in 1808, Marschall von Bieberstein used *A. campestre* in the sense of *A. alyssoides*. The view that *A. parviflorum* is the correct epithet for this species has been followed by a number of authors; however, none has mentioned *Clypeola minor* L. *Flora Monspeliensis*. 21. 1756. In his extensive enumeration of the Linnaean taxa found in the *Dissertationes* and the *Amoenitates Aca-*

*demicae*, Rothmaler (1941) pointed out that *Clypeola campestris* on page 21 of *Flora Monspeliensis* (1756) was to be referred to *Clypeola alyssoides*. What is more important is that Rothmaler recombined *Clypeola minor*, which occurs on the same page, as *Alyssum minus*, but he was wrong in equating it with *A. campestre* (1759), the basionym of which is *Clypeola campestris* (*Sp. Pl.* 2: 650 & 1231. 1753) (cf. Heywood, 1961).

At this point it might prove useful to hypothesize that Linnaeus recognized the confusion surrounding his usage of the epithet *campestre* and attempted to rectify it. In the second edition of *Species Plantarum* he altered the original diagnosis of *Clypeola campestris*, which he had taken from Sauvage, *Methodus Foliorum Monspeliensis*. . . (1751), to read "*calycibus caducis*," thereby hoping to exclude *Clypeola* (*Alyssum*) *alyssoides*, which has persistent sepals. In the same work, attempting to drop the epithet *alyssoides* entirely from use, Linnaeus redescribed *Alyssum alyssoides* as *Alyssum calycinum* from the same type in the Clifford herbarium. Unfortunately, the specimens which Linnaeus (LINN) used to describe *Alyssum campestre* for the second edition of *Species Plantarum* are mixed; among them is a plant (No. 828:10) of *A. alyssoides* which is labelled in Linnaeus's handwriting as *A. campestre*. Except for the type of *A. alyssoides* in the Clifford herbarium, there are no specimens of *Alyssum* now existing which Linnaeus could have used for the first edition of *Species Plantarum*. In the republished version of *Flora Monspeliensis* in the *Amoenitates Academicae* 4. 1759, Linnaeus deleted *Clypeola minor*, which appeared first in the *Dissertationes*, and for it substituted *Clypeola alyssoides*. Though Linnaeus tried to drop the binomial *Clypeola minor* at this point, priority rights must be adhered to, and Rothmaler's combination of *Clypeola minor* as *Alyssum minus* should be accepted as referring to the taxon with deciduous sepals.

In the Dissertation edition of *Flora Monspeliensis*, Linnaeus refers *Clypeola minor* to No. 1138 in Magnol, *Botanicum Monspeliense* (ed. of 1688). Because of the discordant elements in the Linnaean herbarium, none of which can be directly applied as the lectotype of *Clypeola minor*, Magnol's description is accepted as the basis of *Alyssum minus*. In Linnaeus's numbered copy of Magnol's work (Linnean Society, London), No. 1138 is found on page 251 and reads: "Thlaspi Alysson dictum minus capsulis majoribus rotundis, non foliatis; Thlaspi montanum luteum I.B. in priori juxta capsulam quatuor adsunt foliola viridia, in isto vero nulla sunt, capsulae etiam multum differunt; in iisdem locis reperitur, & eodem tempore floret. Addit I.B. Thlaspi montanum minimum Monspeliensium folio laciniato, circa Boutonet collectum, quid sit ignoramus." The two polynomials which Magnol refers to in his circumscription are to be found in J. Bauhin, *Historia Plantarum* 2. 1651. The first of these "Thlaspi montanum luteum . . ." is found on page 928 of Bauhin's work and is accompanied by a figure which can be identified as the taxon commonly referred to as "*Alyssum campestre*," with deciduous sepals and large fruits. This figure cannot be applied to *A. alyssoides* which always has persistent sepals and smaller fruits. The most important character in Magnol's

description is, of course, ". . . capsulis majoribus rotundis, non foliatis . . ." (indicating deciduous sepals), which is clearly contrasted with Sauvage's description of that which became *Clypeola campestre* (*Alyssum campestre*), reading: ". . . calyce persistente . . ." The view is taken here that the Magnol description, "Thlaspi Alysson dictum minus capsulis majoribus rotundis, non foliatis . . ." (but not including his synonyms) constitutes the type of *Clypeola minor* (*Alyssum minus*), and that to take Bauhin's figure as the type would be an unwise extension of the evidence, for this was not the material upon which Magnol's description was based. It may only be taken as additional proof of identity. It is of incidental interest that Magnol's herbarium went to Sauvage, whose herbarium in turn went to Linnaeus. The other polynomial in Bauhin, *Historia Plantarum*, "Thlaspi montanum minimum Monspeliensium folio laciniato," also cited by Magnol, is found on page 929 of Bauhin's work. It is impossible to tell from this description the taxon to which it should be referred. There is no figure.

The establishment of *Clypeola minor* as the basionym of the taxon with deciduous sepals necessitates reducing to synonymy the binomial *Alyssum parviflorum*, which has at one time or another been suggested as the correct name.

*Alyssum campestre sensu lato* as used by many authors (e.g., Busch, 1909) has long been an anomaly with regard to its specific limits. My own interpretation of *A. minus* is in the narrow sense, and is applied to the widespread European and Oriental annual weed with *homomorphic* indumentum (only one type of hair) on the fruits. The taxa with *dimorphic* fruit indumentum of small stellate hairs with appressed or divergent rays in addition to furcate or simple, long and tuberculate hairs (e.g., *A. strigosum* Banks & Solander and *A. hirsutum* Bieb.) are excluded from *A. minus*. In addition to the homomorphic indumentum of fruit and style, the usually smaller, elliptic or ovate, and asymmetrically inflated fruits of *A. minus* var. *minus* distinguish it from *A. strigosum*. Some difficulty may be experienced in distinguishing *A. minus* var. *micranthum* (Meyer) Dudley from *A. strigosum* because of the similarity of their fruits, but the indumentum of the fruits and pedicels is always diagnostic for *A. strigosum*. Though the indumentum of the pedicel of *A. minus* var. *micranthum* frequently appears strigose, this condition is *not* due to the presence of two types of hairs, but to the spreading, divergent and unequal rays of the stellate hairs. The glabrous and shorter styles and the divergent-spreading pedicels of *Alyssum strigosum* are also of value in separating this taxon from *A. minus* var. *micranthum*. It must, however, be stressed that the most reliable diagnostic character of *A. strigosum* is the occurrence of dimorphic indumentum on its fruits and pedicels. This character is easily observed on immature fruits and ovaries, as well as on those which are fully developed.

Although *Alyssum minus* is extremely polymorphic in its habit and fruit size, probably because of the diverse environments in which it grows, the specific limits are no longer as confused as indicated by Rechinger f.

(1953). The exclusion of *A. strigosum* with its dimorphic indumentum allows *A. minus* to be conveniently defined in a narrow sense.

**Alyssum minus** (L.) Rothm. var. **micranthum** (Meyer) Dudley, comb. nov.

*A. micranthum* Meyer, Ind. Sem. Petrop. **1**: 22. 1835(!). Lectotype, Russia. In Campis ad Mare Caspium, Lenkoran, *Meyer s.n.* (LE, non vidi); isotypes (G, W).

*A. campestre* var. *micranthum* (Meyer) Boiss. Fl. Or. **1**: 284. 1867 — *pro parte*(!).

*A. minus* subsp. *micranthum* (Meyer) Briest. Bull. Soc. Bot. Fr. **103**(82 Sess. Extra.): 154. 1956.

DISTRIBUTION AND HABITAT: Sporadically in northern Greece, Crete, North Africa, Crimea, Caucasus, Transcaspian, Turkish and Russian Armenia, northern Turkey, Syria, Lebanon, Israel, Jordan and northern Iran; waste land, cultivated fields and pastures, steppic hillsides, river valleys, forestry plantations, dry south-facing igneous, limestone and gypsum slopes; alt. (30–)500–1600(–2200) m. Fl. (Feb.–) Apr.–June.

The major features distinguishing this taxon from the typical expression of *Alyssum minus* are its larger orbicular fruits, its longer styles, which are only sparsely pubescent, and the coarser and sparser stellate hairs with longer and unequal divergent rays on the fruits, as noted in the following key.

Styles 0.7–1.3 mm. long, covered their entire length with dense, appressed and short-rayed stellate hairs; rays of stellate hairs on fruit overlapping, equal in length, 0.3–0.5 mm. long; fruit elliptic-ovate, 3–4.5 (–5) × 2.5–4 mm., obtuse or rarely emarginate; pedicels ascending; long filaments 0.1–0.8 mm. wide. ..... Var. *minus*.

Styles 1–2 mm. long with sparse, long and divergent-rayed stellate hairs at their bases; rays of stellate hairs on fruit not overlapping, unequal in length, 0.5–1 mm. long; fruit orbicular, 4–7.5 mm. long and wide, emarginate; pedicels horizontal; long filaments 0.3–0.4 mm. wide. .. Var. *micranthum*.

These differential characters of the varieties of *Alyssum minus* are obvious when typical material of each is examined, but in some geographical areas intermediate specimens are quite numerous, i.e., North Africa, Iraq and Iran. In the light of the occurrence of intermediates, and the fact that var. *micranthum* occurs sporadically as small populations, recognition at any rank other than variety would not be justified.

**Alyssum strigosum** Banks & Sol. subsp. **cedrorum** (Schott & Kotschy) Dudley, stat. nov.

*A. cedrorum* Schott & Kotschy, Österr. Bot. Wochenbl. **11**: 169. 1854 (!). Holotype, Turkey, C5: Prov. Icel. In Tauro inter Cedros, *Kotschy s.n.* (cultivated from seed in the Vienna Botanic Gardens, W); isotype (G).

*A. strigosum* var. *cedrorum* (Schott & Kotschy) Briest. Bull. Soc. Bot. Fr. **103**(82 Sess. Extra.): 154. 1956 (!).

DISTRIBUTION AND HABITAT: Found mainly in the Lycian and Cilician Taurus, and extending into Cyprus and northeastern Anatolia. Disturbed and ruderal situations, neglected and cultivated fields, limestone slopes and scree, volcanic plateaus, steppe; often in *Quercus* scrub and *Pinus brutia* woods; alt. 300–1700 m. Fl. Apr.–July.

This taxon was originally thought to be a species distinct from *Alyssum strigosum*, but the presence of a large number of intermediate specimens from Anatolia and Cyprus (mostly occurring within the range of subsp. *cedrorum*) indicates that subspecific rank is more appropriate. The relatively limited distribution of subsp. *cedrorum* is completely contained within the much wider area covered by subsp. *strigosum*. In addition to being a common plant in practically every province of Turkey, subsp. *strigosum* is prevalent throughout southern and eastern Europe, North Africa, and the Levant, extending east into Afghanistan.

The following key indicates the distinguishing characteristics of the subspecies of *Alyssum strigosum*.

Sepals early deciduous; bifurcate hairs on fruit stiff, 0.4–0.6(1) mm. long; styles 0.5–1 mm. long; petals entire or emarginate, 2.5–3 mm. long; fruit 3–5.5 mm. long and wide. . . . . Subsp. *strigosum*.

Sepals persistent; bifurcate hairs on fruit ± sericeous, 1–1.5 mm. long; styles 1–1.5 mm. long; petals bilobed, 4–4.5 mm. long; fruit 5–6.5 × 4–7 mm. . . . . Subsp. *cedrorum*.

**Alyssum trichocarpum** Dudley & Huber-Morath, sp. nov. Holotype, Turkey, *Huber-Morath 9253* (HM); isotype (E). PL. II, FIGS. 12–22.

Affinis *A. cephaloti* Boiss. et *A. xanthocarpo* Boiss. sed a priore racemi elongati (haud globoso-congesti), habitu minus robusto, foliis summam versus decrescentibus haud involucratis, stylo pilis stellatis minoribus et parcioribus differt; a posteriore fructibus minoribus formae diversae et indumento densiore radiis pilorum stellatorum longioribus recedit.

*Planta* annua, patens, e basi multiramosa, (8–)15–20(–30) cm. alta et lata. *Caules* decumbentes vel ascendentes basi haud ramosi, rubro-purpurei. *Folia* post anthesin decidua, sessilia vel breviter petiolata, obovata vel oblanceolata, ad basim sensim attenuata, acuta, 10–15(-20) mm. longa 2.5–4(–7) mm. lata, summum versus decrescentia, pilis stellatis parcis vel densis semper basi tuberculatis radiis antrorse suberectis paucis longis inaequalibus rare ramosis vestita. *Racemus* 5–10 cm. longus, simplex, cylindricus, erectus, in statu florescenti 1–1.5 cm. lato, deinde dense fructiferus apice globoso. *Pedicelli* rigidi, divaricati vel ascendentes, recurvi, 4–7 mm. longi, indumento dimorpho parco vel denso pilis stellatis radiis longis antrorse suberectis inaequalibus et radiis longissime sinuatis sericeis basi tuberculatis inaequalibus tecti. *Sepala* subpersistentia, basi angulato-saccata, subcarinata, margine angusta hyalina, ovata, 3.5–4 mm.

longa, 1 mm. lata, indumento denso dimorpho pilis stellatis radiis longis parcis suberectis et praesertim apicem versus pilis parcis vel multis longissimis antrorse erectis simplicibus vel bifurcatis basi manifeste tuberculatis tecta. *Petala* obovata, basi cuneata, retusa vel bifida, (4–)5–6 mm. longa, 1–2 mm. lata, in unguem sensim attenuata, indumento denso solum pilis stellatis radiis crassis parcis rare ramosis tecta. *Filamenta longa* inaequaliter bilateraliter alatis, 3.5–4.5(–5) mm. longa, ala una quam altera 2-plo latior dentibus minutis 2–3 supra medium provisa, ala altera apicem versus abrupte contracta vel dentata. *Filamenta brevia* 3–4(–4.5) mm. longa, appendice 0.8–1(–1.3) mm. lato, in dimidio inferiore connata. *Glandulae* valde conspicuae globosae. *Stylus* subrostratus, basi manifeste dilatatus, 2–3.5 mm. longus, dense pilosus in dimidio inferiore pilis stellatis minutis radiis paucis brevibus divergentibus praeditus, stigmate magno globoso provisus. *Silicula* duoseminata, pallide flavo-viridia, orbiculata, acuta vel ad basim attenuata (3.5–)4–5(–6.5) mm. longa, 3–4.5 mm. lata, valvis cartilagineis difficiliter separabilibus subcompressis ± aequaliter inflatis indumento denso dimorpho pilis stellatis appressis vel subappressis ramosis radiatis et pilis simplicibus vel bifurcatis (1–)2–3 mm. longis antrorse ascendentibus sinuatis sericeis basi tuberculatis (tuberculis globosis inflatis (1.5–)2.5–3 mm. altis!) provisa. *Ovula* dua per loculum. *Semen* fuscum vel subnigrum, 2.5–3.5 mm. longum, 2–2.5 mm. latum, ala 0.05–0.1 mm. lata, valde crenulata. Fl. May–June, fr. June–July.

**Turkey.** B6: Prov. Malatya, Darende-Akçadağ, ca. 50 km. östlich Darende, Kalkmergel, 1450–1480 m., 20 June 1949, *Huber-Morath 9253* (HM; E). B5: Prov. Yozgat, Akdağmadeni, Aktaş, June 1960, *Curtis 124* (E).

This rare and unusual annual belongs in the species complex of sect. ALYSSUM which includes *Alyssum strigosum* Banks & Sol., *A. xanthocarpum* Boiss., *A. hirsutum* Bieb., *A. bulbotrichum* Hausskn. & Bornm. and *A. cephalotes* Boiss. The new species shares with all of these the annual habit and dimorphic indumentum on the fruit. It may be distinguished from *A. cephalotes*, one of its closest allies, by the elongate fruiting raceme, more reduced form of growth, uppermost leaves which are not involucrate but are smaller than the basal leaves, and indumentum on the style composed of minute stellate hairs only. The new species may be separated from *A. xanthocarpum* by smaller, orbicular fruits with denser indumentum composed primarily of much longer and more strongly tuberculate hairs. *A. trichocarpum* may further be distinguished from all species in the complex by the outwardly arcuate pedicels and the very thick fruit valves separated only with difficulty.

**Alyssum praecox** Boiss. & Bal. var. **albiflorum** Dudley, var. nov. Holotype, Turkey, B5: Prov. Kirşehir, Sifegöl, near Mucur, salt marsh in zone nearest lake, in stiff clay, leaves succulent, flowers white, 17 June 1954, *Davis 21795* (E); isotypes (BM, K).

A typo floribus albis et habitu halophilo differt.

This new variety is a local and extremely halophytic low altitude race which formed a large population in the clay zone nearest the edge of a small salt lake in central Anatolia. It differs from the high altitude typical variety in possessing white flowers and somewhat more succulent leaves (features originally noted on the label). Its distinctness is supported by the additional information that the nearest station of the yellow-flowered typical variety of *A. praecox* lies ca. 100–150 miles to the south in the high mountains of the Anti-Taurus. The habitat of var. *praecox* is predominantly alpine, at altitudes of 1500–2600 meters. The plants of var. *praecox,* more often than not, are found very near the snow line. The distribution of var. *praecox* is that of a typical alpine or montane eastern Anatolian species, extending from the Cilician Taurus to the Armenian Highlands, and occasionally into Turkish Kurdistan. The altitude of the type locality, in the steppe, of var. *albiflorum* is approximately 600 meters. The vegetation present there is predominantly of Irano-Turanian elements, and is similar to that found at most Anatolian salt lakes. The substrate on which var. *praecox* is found is calcareous in nature, or rarely igneous.

Section **Gamosepalum** (Hausskn.) Dudley, comb. & stat. nov.

*Gamosepalum* Hausskn. Mitt. Thür. Bot. Ver. 11: 73. 1897 (!). LECTOTYPE SPECIES: *Alyssum lepidoto-stellatum* (Hausskn. & Bornm.) Dudley.

Series **Connata** Dudley, ser. nov. TYPE SPECIES: *Alyssum lepidoto-stellatum* (Hausskn. & Bornm.) Dudley.

Filamenta longa connata. Indumentum e pilis stellatis pauciradiatis (radiis ramosis) compositum. Petala albida vel pallide flava, limbo basi saepe purpureo-venoso.

**Alyssum lepidoto-stellatum** (Hausskn. & Bornm.) Dudley, comb. nov.

*Gamosepalum lepidoto-stellatum* Hausskn. & Bornm. Mitt. Thür. Bot. Ver. 11: 73. 1897 (!). Holotype, Turkey, A/B 6: Prov. Sivas, in Ponto Australi in declivibus apricis inter Sivas et Mt. Yyldisdagh (Yildis dağ), 1300–1400 m., 6 June 1890, *Bornmüller 1671* (JE, non vidi); isotypes (BM, G).

*Gamosepalum confine* Hausskn. *op. cit.* 74 (!). Lectotype, Turkey, B7: Prov. Erzincan, Chama on Euphrates, 1890, *Sintenis 2161*, (JE, non vidi); isolectotype (K).

DISTRIBUTION AND HABITAT: Turkish endemic from the central and southern steppe areas and calcareous hills; alt. 1300–1524 m. Fl. May–June.

The reasons for recognizing *Gamosepalum* as a section within *Alyssum*, rather than as a distinct genus, will be considered in a later paper.

The type species, *Alyssum lepidoto-stellatum*, is easily separated from *A. paphlagonicum* (Hausskn.) Dudley, with which it has sometimes been confused, by its merely retuse and sparsely pubescent petals, shorter styles,

more spreading usually horizontal pedicels and few-fruited condensed racemes. The habit of *A. lepidoto-stellatum* is more dwarf and caespitose than the mostly erect, luxuriant, and coarse habit of *A. paphlagonicum*.

Schulz (1927) reduced *Gamosepalum confine* to synonymy under *G. lepidoto-stellatum* Hausskn. & Bornm. The lectotype collection of *G. confine* (*Sintenis 2161*) matches *Alyssum lepidoto-stellatum* (Hausskn. & Bornm.) Dudley in all characters except its petals (ca. 6 mm. long), which are nearly as large as the largest found in *A. paphlagonicum*. The other specimen of *G. confine* cited and collected by Haussknecht (Iran, Monte Singara Mesopotamiae, May 1867) has not been seen. Although Haussknecht claims to have been unable to distinguish his specimen from the type of *G. confine* (= *A. lepidoto-stellatum*), from the diagnosis in which he contrasts the Iranian plant with the type of *A. lepidoto-stellatum*, I think he may possibly have had *A. sulphureum* Dudley & Huber-Morath.

**Alyssum paphlagonicum** (Hausskn.) Dudley, comb. nov.

*Gamosepalum paphlagonicum* Hausskn. Mitt. Thür. Bot. Ver. **11**: 74. 1897 (!). Holotype, Turkey, A4/5: Prov. Kastamonu, Paphlagoniae, dist. Kastambuli, in montosis supra Kissiltscha (Kisilia-Kisilca) pr. Tossia, 24 May 1892, *Sintenis 3865* (JE, non vidi); isotypes (BM, G, K).

DISTRIBUTION AND HABITAT: Endemic to central and northeastern Anatolia, in vineyards, serpentine and noncalcareous areas, and *Artemisia* steppe; alt. 800–1372 m. Fl. May–June.

This species is partially sympatric with *Alyssum lepidoto-stellatum*. In addition to the differential characters cited in the discussion of *A. lepidoto-stellatum*, *A. paphlagonicum* possesses several other distinctive characteristics. The sepals of *A. paphlagonicum* show a tendency to be slightly inflated and are separable with difficulty at maturity. Those of *A. lepidoto-stellatum* do not illustrate any obvious inflation and are easily separated at maturity. The overall indumentum of *A. paphlagonicum* is composed of larger and coarser stellate hairs, and the floral parts are, on the average, larger than those of *A. lepidoto-stellatum*. However, on individual specimens the range of variation is too great to allow these species to be safely distinguished on such quantitative characters. *Alyssum paphlagonicum* appears to have an edaphic preference for serpentine or igneous rubble, whereas *A. lepidoto-stellatum* is confined almost entirely to calcareous soils.

**Alyssum thymops** (Huber-Morath & Reese) Dudley, comb. nov.

*Ptilotrichum thymops* Huber-Morath & Reese, Repert. Sp. Nov. **52**: 40. 1943 (!). Holotype, Turkey, C/5: Prov. Niğde, Cappadocien, Steppe bei Bor, Vilajet Niğde, 10 June 1937, *Reese s.n.* (HM); isotype (E).

DISTRIBUTION AND HABITAT: Endemic to central Anatolia in steppe, wheat fields, eruptive stones; in association with *Pinus nigra*; alt. 980–1560 m. Fl. June.

Huber-Morath (1943) correctly points out that his *Ptilotrichum thymops* is morphologically closer to *Gamosepalum lepidoto-stellatum* than any oriental species of *Ptilotrichum* sensu Meyer. He noted, however, that the connate sepals and connate long filaments characteristic of *Gamosepalum* were not found in his *Ptilotrichum thymops*. Examination of the type material of *Ptilotrichum* (*Alyssum*) *thymops* revealed that the fusion of its long filaments, the "pseudo-connation" of its sepals, and its indumentum of few-rayed stellate hairs (not lepidote as indicated by Huber-Morath) were consistent. These features ally it directly to the complex in sect. GAMOSEPALUM (series *Connata*) containing *A. tetrastemon* Boiss., *A. lepidoto-stellatum*, and *A. paphlagonicum*.

*Alyssum thymops*, which is partially sympatric in the central Anatolian steppe with two of its closest allies, *A. tetrastemon* and *A. paphlagonicum*, may be distinguished from these by the weakly dimorphic and sparse short-rayed hairs on the sepals; the obovate, glabrous, pale cream petals; the very narrow linear-oblanceolate leaves; and the noninvolucrate cauline leaves. The narrow wings of the long filaments of *A. thymops* led Huber-Morath to describe "stamina non alata." These wings, which are narrower than those of any other species in sect. GAMOSEPALUM, are of further distinguishing value.

Series **Libera** Dudley, ser. nov. TYPE SPECIES: *Alyssum baumgartnerianum* Bornm. ex. Baumg. Jahresb. Kaiser Franz Josef-Land. Gymn. Oberrealsch. Baden bei Wien **48**: 16. 1911. Lectotype, Lebanon. Libanon, Dschebel Barûk ad nives, 2100 m., 15 June 1910, *Bornmüller 11405* (W); isolectotypes (BM, E, G, K).

A serie *Connatis* filamentis longis contiguis liberis (non connatis), indumento pilis lepidotis multo-radiatis, petalis sulphureis haud purpureovenosis recedit.

**Alyssum corningii** Dudley, sp. nov. Holotype, Turkey, *Dudley* (*D. 35911*) (E); isotypes (A, HM). PL. III, FIGS. 1–11.

*A. tetrastemon* Boiss. var. *cappadocicum* Boiss. Fl. Or. **1**: 278. 1867 (!). Holotype, Turkey, *Balansa 493* (G); isotype (GH) — *non* var. *cappadocica* Boiss. 1842.

*A. tetrastemon* sensu Baumg. Jahresb. Kaiser Franz Josef-Land. Gymn. Oberrealsch. Baden bei Wien **48**: 5. 1911 (!) — *non* Boiss. 1842.

Affinis *A. tetrastemon* Boiss. sed habitu diverso, indumento ex toto fere monomorpho pilis stellatis paucis radiatis brevibus, foliis haud involucratis, racemi elongati multifructi differt.

*Herba* perennis suberecta vel patens, basi multiramosa et suffruticosa, 7–12 cm. alta, 5–10(–15) cm. lata. *Planta* ex toto indumento cinereo-cano e pilis stellatis densis punctatis semper stipitatis interdum manifeste basi tuberculatis 0.2–0.4 mm. latis radiis brevibus vel longis 5–10 radiatis crassiusculis suberectis (rare appressis) inaequalibus multiramosis vel

lepidotis composito. *Caules floriferi* ascendentes vel erecti, 2–7(–12) cm. longi. *Surculi steriles* dense foliati, basi caulium floriferorum conferti, 1–3 cm. longi. *Folia caulium floriferorum* linearia, oblonga vel oblanceolata, acuta, sensim in petiolum attenuata, 6–10 mm. longa, 1.5–2(–2.5) mm. lata; superiora longiora et latiora, ad marginem saepe subhirsuta, non involucrata. *Folia caulium sterilium* lineari-oblanceolata, acuta vel rare obtusa, 6–10 mm. longa, 0.5–1(–1.5) mm. lata, pilis stellatis quam eis foliorum caulium floriferorum densioribus et minoribus. *Racemus* simplex, brevibus, saepe confertus, rare subumbelliformis, post anthesin elongatus, saepe corymbosus ramulis aequalibus 1.8–2(–2.5) cm. longus. *Pedicelli* erecto-patentes, stricti, rigidi, subrecurvi, 3–6 mm. longi, pilis stellatis furcatis et suberectis sicut sepala obsiti. *Sepala* basi subsaccata, lanceolata vel ovata, acuta, 3–3.5 mm. longa, 1–1.5 mm. lata, obscure pseudoconnata ob pilis intertextis cohaerentia, facile separabiles, extus indumento pilis stellatis appressis et rare apicem versus pilis furcatis basi tuberculatis radiis delicatissimis sinuatis inaequalibus sericeis sparse vel dense provisa, intus pilis stellatis radiis delicatulis inaequalibus sericeis obsita. *Petala* in sicco pallida, late spatulata, integra vel subretusa, 4.5–5.5 mm. longa, 1–1.5 mm. lata, infra constrictionem medianem ungue alata (ala denticulata 0.4–0.6 mm. lata) munita, nervo mediano unguis pilis stellatis parcis radiis haud ramosis proviso. *Filamenta longa* 3–4 mm. longa, libera, contigua, bilateraliter anguste marginata, superne sensim contracta, basi vel etiam ad medium rare conniventia sed facile separabiles pilis stellatis parcis minutis provisa. *Filamenta brevia* (1.8–)2–3.5 mm. longa, basi dente brevissimo 0.2–0.3 mm. longo provisa. *Stylus* rostratus vel subrostratus, 1.5–2.5(–3) mm. longus, in dimidio inferiore pilis stellatis minutis multiradiatis parce vel dense provisus. *Silicula* uniseminata vel rare duoseminata, orbicularis, ovata, truncata vel subemarginata, 3.5–4 mm. longa, 2.5–3.5 mm. lata, valvis cartilagineis aequaliter vel inaequaliter inflatis indumento cano dense vestitis. *Ovula* dua per loculum. *Semen* immaturum, alatum. Fl. et fr. June.

DISTRIBUTION AND HABITAT: Entirely confined to the central Anatolian steppe; alt. 1050–1500 m.

**Turkey.** B4: Prov. Ankara, Giarrkale bei Haymana, Berg Steppe, *Kotte 1165* (K). B5: Prov. Niğde, Tuff bei Niğde, 1100 m., 4 June 1898, *Siehe 60* (B, BM, G, K, W). C4: Konya to Sultanhani on new road, 18 miles from Konya, 1050 m., in new enclosed forestry plantation, steppic habitat, pale lemon flowers, rare, 16 June 1962, *Dudley* (*D. 35911*) (E; A, HM); Steppen bei Divle (Karaman-Ereğli), 1300 m., June 1906, *Siehe 241* (E); Sarayönü, civari Step yel Lenari, May 1943, *Birand s.n.* (ANK). C5: Prov. Seyhan, Partie superieure de la Vallee du Kamechly-Tchai (Keamşli), 1490–1500 m., 16 June 1856, *Balansa 493* (G, GH).

*Alyssum corningii* was first described as *A. tetrastemon* var. *cappadocicum* by Boissier (1867), who differentiated it from the typical *A. tetrastemon* because it possessed ". . . pili omnes lepidoti et caules saepe ramulosi." This description may be contrasted with "basi suffrutescens lepi-

dotum et insuper breviter tomentoso-hirtum caulibus humilibus . . . ," given by Boissier (1867) for *A. tetrastemon* sensu stricto. Boissier's var. *cappodocicum*, of 1867, is antedated by his var. *cappadocica*, of 1842, which was based on a different type and is obviously a synonym of *A. tetrastemon* sensu stricto.

The indumentum of *Alyssum corningii* is for the most part monomorphic and appressed and is lepidote in the lower portions of the plant. That of *A. tetrastemon* is dimorphic and distinctly hirsute and is tomentose especially on the sepals, pedicels, and upper stems and leaves. Baumgartner (1911, pp. 5, 6) stated that the indumentum difference did not justify describing a new species. In fact, Baumgartner had only the *Siehe 60* collection of *A. corningii* at his disposal. However, examination of all available material indicates that the indumentum character is of differential value when combined with the other consistent diagnostic characters. Accordingly, Boissier's var. *cappadocicum* of 1867 should be maintained as a distinct species.

In addition to the characters detailed by Boissier, *Alyssum corningii* may be separated from *A. tetrastemon*, the taxon with which it is most easily confused, by the closely adjacent and overlapping, but free long filaments (rarely connate at their bases), the narrower cauline leaves which are not involucrate, and the many-fruited, elongate racemes.

The distribution and general ecology of *Alyssum corningii* and *A. tetrastemon* do not appear to be mutually exclusive, though they have never been found growing together. Both species probably represent branches from a common ancestor within the perennials of sect. ALYSSUM and are closely allied to *A. iranicum* Baumg., *A. aizoides* Boiss., *A. bornmuelleri* Hausskn. ex Degen, *A. doerfleri* Degen, *A. taygeteum* Heldr., and *A. caespitosum* Baumg.

The specific epithet of this new taxon honors a friend and benefactor, the Honorable Erastus Corning II, of Albany, New York, whose support and interest made my investigations of *Alyssum* at Edinburgh a reality.

**Alyssum sulphureum** Dudley & Huber-Morath, sp. nov. Holotype, Turkey, *Huber-Morath 11969* (HM); isotype (E). PL. IV, FIGS 13–26.

*Gamosepalum paphlagonicum* sensu Bornm. Symb. Fl. Anat. 59. 1936, pro parte quoad plantam Mesopotamiam a Handel-Mazzetti lectam — non Hausskn. (!).

Affinis *A. bornmuelleri* (sect. ALYSSUM), *A. aizoidi* (sect. ALYSSUM) et *A. harputico* Dudley (sect. GAMOSEPALUM), sed ob omnibus speciebus habitu diverso, sepalis angustioribus margine membranaceo, appendice filamentorum brevium multo breviore differt; insuper a primo forma squamorum lepidotorum, petalis retusis vel bilobatis recedit; a secundo filamentis longis edentatis, unguibus petalorum pilis stellatis provisis divergit; a tertio indumento diverso, petalis majoribus, pilis stellatis forma foliorum distinguitur.

*Herba* perennis, suffruticosa, dense caespitosa, pusilla, multiramosa, sed ad basim efoliata, (5–)10–20 cm. alta. *Planta* ex toto indumento denso appresso cinereo-argenteo squamis minute punctatis lepidotis (0.2–)0.3–0.5 mm. diametro vestitis, sed superne et in marginibus (rare in paginis ambobus) foliorum superiorum indumento ut in sepalis dimorpho obsita, pedicellis et sepalis pilis stellatis radiis longis sericeo-villosis vestitis. *Caules floriferi* erecto-ascendentes, parce foliati, (2.5–)8–10 cm. longi. *Surculi steriles* numerosi, densissime conferti, patentes, dense foliati, 1.2–5 cm. longi. *Folia caulium floriferorum* lineari-oblanceolata, sessilia, acuta, (5–)10–15 mm. longa, 1.5–2(–2.5) mm. lata, ascendentes, superiora sensim increscentia, post anthesin decidua; summa involucrata. *Folia caulium sterilium* oblanceolata vel subspatulata, acuta, (2–)6–10 mm. longa, 1.5–2 mm. lata. *Corymbi* umbelliformes capitato-rotundati, congesti, 1.5–2 cm. longi et lati, floribus 5–15. *Pedicelli* in statu fructifero 3–4.5(–6) mm. longi, crassi, rigidi, ascendentes vel subhorizontales, indumento dimorpho eo sepalorum simili dense obtecti. *Sepala* subpersistentia, apice cucullata, inaequalia, acuta, pseudoconnata, (3.5–)4.5–5.5 mm. longa, (1.5–)2–3 mm. lata, margine hyalina angusta, 0.1–0.2 mm. lata squamis lepidotis tecta in dimidio inferiore intertexto connata, extus squamis lepidotis minute punctatis argentis 0.3–0.4 mm. diametro apicem versus indumento dimorpho e pilis stellatis basi tuberculatis sericeo-villosis radiis inaequalibus longis paucis vel numerosis 0.5–1 mm. longis squamis lepidotis composito, intus indumento dimorpho parce vel dense obtecta e pilis stellatis radiis sericeis valde inaequalibus duobus longis antrorse appressis et pilis stellatis radiis aequalibus brevibus composito. *Petala* sulphurea, late spatulata, retusa vel bilobata, (5.5–)6–8 mm. longa, 2.5–3 mm. lata; unguis ad medium constrictus alis latis membranaceis saepe integris, nervo mediano pilis stellatis sublepidotis radiis paucis vel multis suberectis dense vel sparse obsito. *Filamenta longa* 4.5–5.5(–6) mm. longa, libera, non connata sed verum contigua, edentata, anguste bilateraliter alata, ad basim sensim dilatata. *Filamenta brevia* 3–4.5 mm. longa, angustissime alata ad basim appendice brevissima minuta praedita. *Antherae* auriculatae, apice acutae, 1 mm. longae. *Stylus* in statu fructifero, tenuis ad basin dilatatus, (2–)3–3.5(–4) mm. longus, glaber vel in dimidio inferiore pilis stellatis radiis suberectis obsitus. *Silicula* uniseminata, rare duoseminata, orbiculata vel obovata, truncata vel obtusa, (4–)5–5.5(–6) mm. longa, 3.5–4.5 mm. lata, valvis cartilagineis manifeste inaequaliter inflatis indumento denso argenteo e squamis appressis minute punctatis lepidotis vel sublepidotis multiradiatis 0.3–0.5 mm. diametro composito obsitis. *Ovula* dua per loculum. *Semen* pallide brunneum, 3.5–4 mm. longum, 3 mm. latum, ala angusta (0.05–)0.1–0.2 mm. lata. Fl. June, fr. July.

DISTRIBUTION AND HABITAT: Southeastern Anatolia and northern Syria and Iraq, on limestone and marl ledges, steppe hillsides, and scree; alt. 600–1650 m.

**Turkey.** B6: Prov. Malatya, Kalkmergelhügel östlich ob Darende, 1000–1050 m., 28 June 1953, *Huber-Morath 11969* (HM; E); Mergelhügel, 2 km. westlich

ob Darende, an der Strasse nach Gürün, 1090 m., 28 June 1953, *Huber-Morath 11970* (HM); Mergelhügel nördlich ob dem Dorf Darende, 950–980 m., 20 June 1949, *Huber-Morath 9252* (HM); entre Derindeh et Kavak Aghatch (Akçadağ), 14 June 1906, *Post 52* (G). C9: Prov. Hăkâri, mons Bestabije (Beytüşşebap) prope Hoz, Amadia (Imfiya)-Sattak (Çatak), 1650 m., July 1910, *Nâbélek 1264* (BRA). **Northern Syria.** Desert nr. Marbat Antar, 3 May 1900, *Post s.n.* (BM). **Northern Iraq.** Kalk-Hänge bei Dorfruine Chara (Bir Garan) im Dschebel Abd'elasis (Debel-Abdul Aziz), 600 m., *Handel-Mazzetti s.n.* (W).

The closest ally to this new species in sect. GAMOSEPALUM is probably *Alyssum harputicum* Dudley. *Alyssum sulphureum* may be separated from it easily by the caespitose, dense cushion-forming habit, broader and shorter leaves, smaller lepidote scales with longer peripheral rays on the sterile shoot leaves and fruits, larger and usually bilobed petals, and the narrower membranous sepal margins. In addition, the stellate hairs on the upper cauline leaves, pedicels, and sepals often appear strigose with long, unequal and spreading rays. This form of indumentum is shared with *A. bornmuelleri* and *A. aizoides* in sect. ALYSSUM, from which *A. sulphureum* may be separated by the same characters which distinguish it from *A. harputicum*. The edentate long filaments and the presence of indumentum on the petals are also of differential value in separating the new species from *A. aizoides*.

Considerable difficulty was experienced in placing *Alyssum sulphureum* in the correct section due to its resemblance to some species of sect. ALYSSUM. The problem was clarified by observation on *A. sulphureum* of dimorphic sepals which, because of their interlocking indumentum, appear fused; copious indumentum on the inner surface of the sepals; and edentate, free but adjacent and overlapping, long filaments.

Haussknecht (1897) was bewildered by this resemblance of *Gamosepalum* to *Alyssum* and discussed it at length when he proposed the binomial *Gamosepalum alyssoides*. However, in any case, the specific epithet *alyssoides* may not be used for any taxon in *Alyssum* other than *A. alyssoides* (L.) L. (1759), a combination based on *Clypeola alyssoides* L. (1753). Haussknecht proposed that the name *Gamosepalum alyssoides* should be applied if, with the examination of additional material, it became evident that the three species he described (*G. lepidoto-stellatum*, *G. confine*, and *G. paphlagonicum*) did not warrant specific recognition. These three species would, according to him, then be reduced to the rank of varieties under *G. alyssoides*. It is interesting that the many additional collections of *Gamosepalum*, since the time of Haussknecht's descriptions, indicate that *G. lepidoto-stellatum* and *G. paphlagonicum* are distinct species and well differentiated from one another. *Gamosepalum confine*, however, as Schulz (1927) points out, must be treated as synonymous with *G. lepidoto-stellatum*.

**Alyssum harputicum** Dudley, sp. nov. Holotype, Turkey, B7: Prov. Elâziğ, Armenia Turcica, Kharput (Harput) in summo monte Kisil

Depe, 10 May 1889, *Sintenis 323* (G); isotypes (K, W) (all as *A. aizoides*). PL. IV, FIGS. 1–12.

*A. aizoides* sensu Baumg. Jahresb. Nied.-Öst. Land.-Lehrers. Wien.-Neust. **36**: 24. 1909 et sensu Bornm. Symb. ad Fl. Anat. 54. 1936 — non Boiss.(!).

Affinis *A. lycaonico* (Schulz) Dudley sed squamis lepidotis duplo minoribus, caulibus longioribus ascendentibus, foliis surculorum sterilium angustioribus, sepalis haud inflatis minoribus, petalis minoribus indumento parciore differt.

*Herba* perennis e basi ramosa suffruticosa. *Planta* ex toto squamis appressis disciformibus albo-lepidotis punctatis 0.2–0.3 mm. latis dense vestita. *Caules floriferi* erecti vel arcuato-ascendentes, 5–11 cm. longi. *Surculi steriles* numerosi eoque caespitosi, fastigiati, ascendentes, 1–4 cm. longi, dense foliati. *Folia caulina* sessilia, acuta; inferiora obovato-oblanceolata, ca. 4 mm. longa, 1--1.5 mm. lata; mediana linearia vel linear-cuneata, ca. 10 mm. longa, 0.5–1 mm. lata. *Folia surculorum sterilium* lineari-oblanceolata, 5–10 mm. longa, 0.5–1 mm. lata. *Corymbi* simplices vel pauci-ramosi, congesti, rotundati, 1.3–1.5(–2) cm. lati, foliis caulinis summis subinvolucrati. *Pedicelli* patentes vel erecti, ca. 5 mm. longi. *Sepala* persistentia, pseudoconnata, subcarinata, subinaequalia, apice cucullata, acuta, 2.5–4 mm. longa, 1–1.5 mm. lata, margine hyalina squamis tecta, in dimidio inferiore ob indumento intertexto cohaerentia, extus dense lepidota, intus pilis radiis valde inaequalibus duobus longis antrorse appressis et pilis stellatis radiis aequalibus brevibus vestita. *Petala* lutea, obovata vel spatulata, 5–5.5 mm. longa, 2 mm. lata, apice integra vel leviter retusa, unguis margine hyalina in parte superiore dilatata, 0.2–0.3 mm. lata, pilis stellatis paucis obsitus. *Filamenta longa* ca. 4 mm. longa, libera, sed verum contigua, edentata, bilateraliter membranaceo-marginata, superno sensim contracta. *Filamenta brevia* 3–3.5 mm. longa, basi appendice brevissima praedita. *Glandulae* prominentes, globosae. *Antherae* 0.8–1 mm. longae. *Ovarium* orbiculare, 2 mm. longum, 1.5 mm. latum, dense lepidoto-squamatum, apice emarginatum. *Ovula* dua per loculum, non marginata. *Stylus* in statu florescenti 2.5–3 mm. longus ad basin dense lepidotus stigmate globoso capitato provisus. *Fructus* ignotus. Fl. May.

The diagnostic characters separating *Alyssum harputicum* from *A. lycaonicum* are easily observed, and, although these species are widely separated geographically, they appear to be closely related. *Alyssum lycaonicum* has large and extremely inflated sepals enclosing the ovary or fruit (presumably of dispersal value), whereas *A. harputicum* has persistent but considerably smaller sepals which are never inflated. The petals and lepidote scales of both species are similar in form, but those of *A. harputicum* are always smaller. The narrow, almost needle-like, involute leaves of *A. harputicum* are unique in sect. GAMOSEPALUM. Similar leaves, however, are possessed by *Alyssum* (*Triplopetalum*) *pinifolium* (Nyár.) Dudley (sect. ODONTARRHENA), an example of parallel evolution in morphologically and taxonomically widely separated species.

Baumgartner (1909, p. 24) erroneously thought the type collection of *Alyssum harputicum* represented *A. aizoides* Boiss. in sect. ALYSSUM. Unfortunately he did not examine any material in addition to *Sintenis 323* and did not know *A. aizoides* sensu stricto, but relied on a Stapf determination. Bornmüller (1936) repeated this error but stated "folia linearia," accordingly including *A. harputicum* within *A. aizoides*. *Alyssum harputicum* is so distinct morphologically that it should never be confused with any other species, even its closest ally.

**Alyssum niveum** Dudley, sp. nov. Holotype, Turkey, B3: Prov. Eskişehir, distr. Sivrihisar, nordöstlich von Yaka Pinar, Steppe auf Kalk, 18 May 1941, *Romieux s.n.* (HM). PL. III, FIGS. 12–20.

Affinis *A. harputico* Dudley sed habitu valde diverso, foliis latioribus, petalis longioribus et squamis lepidotis maioribus differt.

*Herba* perennis, caespitosa, conferta, 3 cm. alta, 5 cm. lata. *Planta* ex toto indumento manifeste albo-argenteo squamis lepidotis multiradiatis appressis disciformibus manifeste punctatis (0.1–)0.2–0.5(0.7) mm. diametro dense vestita. *Folia* imbricata, summam versus accrescentia, sessilia, acuta, squamis lepidotis 0.4–0.5 mm. diametro dense obtecta; superiora involucrata, linearia, oblanceolata vel spatulata, 10–15 mm. longa, 2–3 mm. lata; inferiora lanceolata vel obovata, 7–10 mm. longa, 2–2.5 mm. lata. *Corymbi* simplices, conferti, umbelliformes, 1–2 cm. lati et longi, floribus 8–15. *Pedicelli* in statu florescenti subhorizontales vel divergentes, interdum deflexi, 3–4 mm. longi, indumento denso squamis lepidotis 0.4–0.5 mm. diametro tecti. *Sepala* lanceolata vel elliptica, obtusa vel subacuta, basi subsaccato-angulata, leviter dimorpha, pseudoconnata sed facile separata, in dimidio inferiore ob indumento intertexto cohaerentia, persistentia, (3–)3.5–4.5 mm. longa, (1.5–)2.5–3 mm. lata, margine hyalina 0.2–0.3 mm. lata, extus indumento denso squamis lepidotis 0.2–0.3 mm. diametro provisa, intus pilis stellatis appressis multiradiatis sublepidotis parce vel copiose munita. *Petala* spatulata, retusa vel subretusa, rare integra, flava, 6.5–7 mm. longa, 3–3.5 mm. lata, in ungue sensim attenuata vel ad medium constricta margine unguis saepe denticulata, squamis lepidotis 0.1–0.2 mm. latis in ungue (rare in lamina) obsita. *Filamenta longa* libera sed verum contigua, interdum omnino conniventia, angustissime bilateraliter alta, ad basim leviter dilatata, edentata, 3.5–4 mm. longa. *Filamenta brevia* 2.5–3 mm. longa, ad basim leviter dilatata, basi appendice brevissimo provisa. *Glandulae* minutae, globosae, lobatae. *Antherae* 1 mm. longae, apice obtusae vel subacutae, connectivo prolongato 0.2–0.3 mm. longo. *Ovarium* orbiculato-ovatum, apice emarginatum, 1.5–2.5 mm. longum, 1–2 mm. latum, indumento denso albo squamis lepidotis 0.4–0.5 mm. diametro provisum. *Ovula* dua per loculum, ut videtur solum una vel dua maturantes. *Stylus* in statu florescenti 2–2.5(–3) mm. longus, rigidus, ad basim dilatatus, in dimidio inferiore (rare ex toto) squamis lepidotis densis provisus, stigmate magno globoso provisus. *Fructus* ignotus. Fl. May.

A detailed comparison of the species in sect. GAMOSEPALUM shows that *Alyssum niveum*, a very rare steppe species, is morphologically closest to *A. harputicum*. *Alyssum niveum* deviates from *A. harputicum* in its extremely reduced habit, wider leaves, and larger lepidote scales. The petals of *A. niveum* are also distinctive in being very large and usually retuse, and in frequently having denticulate wings on the claws. The petals of *A. harputicum* are smaller and have entire claw wings.

Unfortunately, the species is known only from the type collection of one plant, but the numerous morphological discontinuities which distinguish it from the other species in sect. GAMOSEPALUM indicate that specific rank is appropriate. It is hoped that future collectors will rediscover this beautiful species. I was not successful in finding it in an area near the type locality.

**Alyssum lycaonicum** (Schulz) Dudley, comb. nov.

*Gamosepalum lycaonicum* Schulz, Notizbl. Bot. Gart. Mus. Berlin **10**: 110. 1927 (!). Holotype, Turkey, B3: Prov. Konya, Wilajet Konia, Steppe bei Korasch (Koraşi) in Lykaonien, 1400 m., June 1906, *Siehe 274* (B, non vidi); isotype (BM).

DISTRIBUTION AND HABITAT: Rare Anatolian endemic, confined to the dry steppe near Konya; alt. 1400 m. Fl. June.

The morphological discontinuities which define the limits of this species are of such significance that there should be no confusion with any other. The homomorphic indumentum of very large disciform lepidote scales (up to 2 mm. in diameter), the extremely inflated and enveloping calyx, the erect and tall growth, and the noninvolucrate cauline leaves which decrease in size upwards are sufficient to distinguish the species clearly from *Alyssum harputicum* and *A. niveum*, its closest allies. The distribution of these three species is completely allopatric.

This "*Gamosepalum*" was described as having deep yellow petals, a character which invalidated the original generic criterion of white petals (Schulz, 1927). However, *Alyssum baumgartnerianum*, designated by me as the type species of series *Libera* in sect. GAMOSEPALUM, also has deep yellow petals.

Section **Odontarrhena** (Meyer) Koch, Synop. Fl. Germ. Helv. 59. 1836. LECTOTYPE SPECIES: *Alyssum tortuosum* Waldst. & Kit. ex Willd. Linn. Sp. Pl. ed. 4. 3(1): 466. 1800. [Waldst. & Kit. Pl. Rar. Hung. 1: 94. *t. 91.* 1802.] Lectotype, Hungary. In arenosis sterilissimis Hungariae (PR, *Herb. Waldstein no. 502369*).

Subsection **Inflata,** subsect. nov. TYPE SPECIES: *Alyssum tortuosum* Waldst. & Kit. ex Willd.

Silicula dehiscentia, pedicello rigido suffulta, valvis fere inflatis (aequalibus vel inaequalibus) vel raro subcompressis non undulatis vel conspicue nervosis.

**Alyssum discolor** Dudley & Huber-Morath, sp. nov. Holotype, Turkey, *Huber-Morath 11755* (HM); isotype (E). PL. V, FIGS. 1–11.

Affinis *A. syriaco* Nyár. et *A. chondrogyno* Burtt, sed ab omnibus speciebus habitu altiore et magis diffuso, inflorescentia maiore ramis longioribus divergentibus provisa, foliis maioribus petiolatis longioribus, et fructibus late ellipticis vel obovatis coriaceis rugosis glabris basi longe attenuatis stipitatis differt; a priore appendice diversa filamentae longae recedit; a posteriore (cui probabiliter magis affinis) forma et amplitudine fructuum distinguitur.

*Planta* perennis, pulchra, erecta, suffruticosa, supra basin multiramosa, ramis tenuibus subflexuosis. *Caules floriferi* erecti, 25–40 cm. longi, parce foliati, basi flavescenti-rubri, pilis stellatis parcis multiradiatis brevibus inaequalibus tecti. *Surculi steriles* erecti, e basi lignosi caulium floriferorum ascendentes, basi efoliati, 5–10 cm. longi, supra medium foliati, indumento denso cano obtecti. *Folia* conspicue bicolorata; pagina superior atrovirens pilis stellatis punctatis minutis appressis multiradiatis sparsis vestita; pagina inferior indumento denso albo-cano e pilis stellatis 15–20 radiatis tenuibus delicatulis appressis punctatis 0.2–0.3(–0.4) mm. diametro composito vestita. *Folia caulium floriferorum* divergentes rare subhorizontales, superne sensim decrescentia; inferiora obovata, spatulata, obtusa (15–) 20–35 mm. longa, (4–)6–8 mm. lata, petiolis 5–10 mm. longis; superiora oblanceolata vel anguste obovata, breviter petiolata (7–)8–10(–15) mm. longa, 1–2 mm. lata; summa subbracteata, oblanceolata, acuta, 8–10(–15) mm. longa, 1–1.5 mm. lata. *Folia caulium sterilium* stricte divergentia interdum deflexa, obovata, spatulata, obtusa, 1–20 mm. longa, 3–5(–6) mm. lata, petiolis 4–8 mm. longis. *Corymbi* 7–15(–18) cm. alti et lati, e ramis multis divergentibus vel stricte ascendentibus 3–5(–8) cm. longis compositi; inflorescentiae ultimae subumbelliformes vel in statu fructifero elongatae. *Pedicelli* tenues saepe filiformes, divergentes, 4–6.5 mm. longi, pilis stellatis appressis punctatis minutis multiradiatis valde parce muniti. *Sepala* membranacea, manifeste nervosa, lanceolata vel anguste ovata, basi subsaccata, obtusa, 3 mm. longa, 1 mm. lata, indumento pilis stellatis paucissimis appressis vel subappressis punctatis minutis brevibus paucis vel multis ca. 0.2 mm. diametro radiis saepe ramosis. *Petala* obovata, clavata, integra vel emarginata vel subemarginata, 3.5–4 mm. longa, 1 mm. lata, glabra. *Filamenta longa* 3–4 mm. longa, haud alata, appendice unidentata 1–1.5 mm. longa, basi connata. *Filamenta brevia* 2–2.5(–3) mm. longa, appendice libera lineari-lanceolata acuta vel minute bi- vel tridentata 1.5–2 mm. longa. *Glandulae* inconspicuae, minutae. *Antherae* 0.8–1 mm. longae, auriculatae, apice acutae vel subobtusae. *Ovarium* 1–1.5 mm. longum, 0.5–0.7 mm. latum, oblongo-ellipticum, acutum, glabrum. *Ovulum* unum per loculum. *Stylus* erectus tenuis, 2–2.5 (–3) mm. longus, glaber, stigmate magno capitato 0.2–0.3 mm. diametro provisus. *Silicula* late elliptica vel obovata (rare orbiculata) (5.5–)6–6.5 mm. longa, (2.7–)3–4 mm. lata, stipitata, basi longissime attenuata, stipite (0.5–)1–1.5 mm. longo, valvis coriaceis aequaliter inflatis, glabris manifeste rugosis promi-

nenter nervosis. *Semen* immaturum ut videtur anguste alatum. Fl. Apr.–May, fr. May–June.

DISTRIBUTION AND HABITAT: Rare endemic of southwest Anatolia found on limestone and sandstone cliffs and scree (rarely serpentine); often associated with *Pinus brutia* and *Smilax*; alt. 0–300 m.

**Turkey.** C2: Prov. Muğla, Marmaris, 30 m., *Pinetum brutiae* on serpentine, 24 Mar. 1956, *Davis 25246* (E); Hisarönü, Marmaris-Datça, 80–100 m., saxatile on dry sandstone rocks, uncommon, 6 June 1962, *Dudley* (*D. 35410*) (E); Muğla-Marmaris, 5 km. from Marmaris on descent from high pass, 150–200 m., common saxatile, forming dense thick clumps on limestone cliffs and scree, 3 June 1962, *Dudley* (*D. 35391*) (E); hills on south side of Marmaris village, 100 m., common forming dense clumps under *Pinus brutia* and *Smilax*, 7 June 1962, *Dudley* (*D. 35458*) (E). C3: Prov. Antalya, Bucht von Adrasan am Südfuss des Tahtali dağ (as "Çalbali dağ") zwischen Çirali und Finike, Macchie auf Kalk, 0–300 m., 27 May 1950, *Huber-Morath 11755* (HM; E).

*Alyssum discolor* is in the complex of perennial species including *A. corsicum* Duby, *A. masmenaeum* Boiss., *A. syriacum* Nyár., *A. troodi* Boiss., and *A. chondrogynum* Burtt, all of which have glabrous or glaucous fruits (rarely papillose and never with an indumentum of stellate hairs) and broadly spathulate or obcuneate, often bicolorous, sterile shoot leaves.

The new species, *Alyssum discolor*, differs from its allies, *A. syriacum* and *A. chondrogynum*, in being a more spreading plant, larger in all parts, and with broadly elliptic or obovate, rugose, basally long-attenuate and stipitate fruits. Furthermore, *A. discolor* may be separated from *A. syriacum* by the long basally connate appendage of the long filaments; and from *A. chondrogynum*, to which it is probably most closely related, by the shape and size of its fruits which are lacking in papillae.

A recent gathering of *Alyssum discolor* (*Dudley; D. 35410*) has broadly elliptic fruits somewhat larger than the obovate ones of the type material (PL. V, FIGS. 1 & 2). In all other characters, however, this collection corresponds exactly with the type gathering of *Huber-Morath*. An additional gathering (*Dudley; D. 35458*), collected in close proximity, has fruits exactly matching those of the type specimen. These collections indicate that the shape and size of the fruits of this species are subject to marked variation.

This beautiful chamaephyte is endemic to only a few localities in southwestern Anatolia and exhibits a preference for calcareous situations and low altitudes. One gathering (*Davis 25246*) indicates "serpentine," but it is notable that these specimens are poorly developed and somewhat depauperate compared to populations from calcareous substrates. Most of the plants examined in the field formed large, woody, and saxatile clumps on limestone cliffs near the sea or on calcareous rubble under *Pinus brutia*.

**Alyssum davisianum** Dudley, sp. nov. Holotype, Turkey, *Davis 36799* (E); isotypes (A, HM). PL. I, FIGS. 14–22.

Affinis *A. sibirico* Willd. sed in omnibus partibus minor, fructibus glabris, foliis angustioribus, indumento foliorum pauciori dissimili differt.

*Planta* perennis, caespitosa, 4–10 cm. alta et lata, in sicco lutescens, e basi multiramosa aphylla, lignosa, rubra, cicatrice prominenti foliorum, ex toto indumento virescenti vel cinereo, e pilis stellatis appressis punctatis 4–6 radiatis radiis ramosis aequalibus 0.3–0.6 mm. diametro composito. *Caules floriferi* tenues, ascendentes vel erecti, 4–8 cm. longi, parce foliati, ad basin efoliati, pilis stellatis radiis ± longis ramosis sparse vel dense tecti. *Surculi steriles* apici dense foliati, e basi lignoso caulium floriferorum ascendentes, basi efoliati, 1–2.5 cm. longi. *Folia caulium floriferorum* oblanceolata, obtusa vel subacuta, descrescentia summam versus, post anthesim decidua, involucrata, flavo-virescentia, 7–10 mm. longa, 1–2 mm. lata. *Folia surculorum sterilium* lineari-oblanceolata vel spatulata; inferiora superioribus longiore, 5–8 mm. longa, 1–1.5 mm. lata; superiora dense imbricata, 3–5 mm. longa, 0.5–1 mm. lata. *Corymbi* ramosi, parviflori, ca. 2–5 cm. longi et lati, ramulis stricto ascendentibus vel patentibus, corymbis secundariis subumbelliformibus. *Pedicelli* tenues, rigidi, divergentes vel horizontales, rare deflexi, inter se 1–2 mm. distantes, 3–4 mm. longi, pilis stellatis appressis vel subappressis parce vel copiose provisi. *Sepala* decidua, membranacea, ad apicem carinata, cucullata, ovata, obtusa, 1–1.5 mm. longa, 0.5–0.8 mm. lata, anguste hyalino-marginata, pilis stellatis sparsissimis provisa. *Petala* in sicco aurea, obovata, integra vel retusa, in unguem sensim attenuata, glabra vel solum in ungue pilis stellatis provisa, 2 mm. longa, 0.5–0.7 mm. lata. *Filamenta longa* ca. 1 mm. longa, recurva; appendix bidentata vel acuta, in dimidio inferiore ad filamentum connata, apice libera, 0.3–0.5 mm. longa. *Filamenta brevia* 0.5–1 mm. longa, recurva; appendix libera, lanceolata, filamentum subaequans, apice bidentata vel acuta, 0.2–0.3 mm. lata. *Glandulae* conspicuae, globosae. *Antherae* minutae, 0.3–0.6 mm. longae. *Ovarium* orbiculatum, emarginatum, 0.5–0.7 mm. longum et latum, glabrum sed minute papillosum, translucens, flavo-viride. *Stylus* glaber, tenuis, rigidus, 0.5–1 mm. longus, stigmate leviter dilatato provisus. *Silicula* ut videtur uniseminata, orbiculata, emarginata, 2–3 mm. longa et lata, valvis membranaceis prominenter nervosis glabris laevigatis valde inaequaliter inflatis. *Ovulum* unum per loculum. *Semen* immaturum non alatum. Fl. June–July.

**Turkey.** B2: Prov. Kütahya, Murat dağ, above Gediz, above Kesit Sögüt, 1900 m., rocky igneous slopes, flowers bright yellow, 5 July 1962, *Davis 36799* (A, E, HM); between Kesit Sögüt and Hamam, 1400 m., on metamorphic rocks, 5 July 1962, *Davis 36862* (A, E).

*Alyssum davisianum* does not appear to be closely allied to any known species in sect. ODONTARRHENA, although it resembles *A. sibiricum* Willd. in the orbicular and extremely asymmetrically inflated fruit which has an S-shaped configuration in cross section. It differs strongly from *A. sibiricum* and the closest allies of that species (*A. borzaeanum* Nyár. and *A. caliacrae* Nyár.), in the reduced cushion-forming habit, the prominent

lignose base with copious and raised leaf scars; the much shorter and fewer-fruited corymb; the smaller and always glabrous fruit; the smaller and linear leaves; the indumentum of few-rayed, minute and appressed stellate hairs; and the yellowish-green aspect of the plant. Furthermore, *A. davisianum*, as a restricted endemic, has a preference for igneous or metamorphic substrates, whereas *A. sibiricum* is an extremely widespread and polymorphic species usually found in calcareous situations.

This new species is named in honor of the collector, Dr. P. H. Davis, of the University Department of Botany, Edinburgh, Scotland, whose energy and careful attention as the author's supervisor has always been inspiring.

**Alyssum huber-morathii** Dudley, sp. nov. Holotype, Turkey, *Khan, Prance & Ratcliffe 256* (E); isotype (K). PL. V, FIGS. 12–23.

Affinis *A. fallacino* Hausskn. (syn. *A. baldaccii* Vierh. ex Nyár.) et verosimiliter *A. murali* Waldst. & Kit. (sensu *A. chlorocarpum* Hausskn.) sed ab ambobus habitu valde suffruticoso, foliis caulium fertilium et sterilium manifeste conduplicatis et valde argenteis, fructibus minoribus ellipticis vel anguste obovatis indumento parciore differt; a priore corymbis ultimis umbelliformibus (haud elongatis), pedicellis brevioribus tenuioribus recedit; a posteriore stylo tenuiore, seminibus angustissime alatis (haud late alatis) divergit.

*Planta* perennis, valde suffruticosa, a basi multiramosa. *Caules floriferi* stricti-ascendentes, parce foliosi, 18–25(–35) cm. alti, a basi rubro-purpurei indumento parce summam versus magis conspicuo. *Surculi steriles* dense foliati, erecto-ascendentes vel laxe patentes, 8–16 cm. longi. *Folia caulium floriferorum* lineari-oblanceolata, acuta vel subobtusa, conduplicata, recurva, virescentia, post anthesin decidua, 10–15(–20) mm. longa, 1.5–2 mm. lata. *Folia caulium sterilium* lineari-oblanceolata, acuta, manifeste conduplicato-sulcata, (4–)10–20(–25) mm. longa, 1–1.5(–2.5) mm. lata, indumento dense lepidoto e pilis albis argenteis minute punctatis 15–20(–30) radiatis multo ramosis 0.4–0.5 mm. diametro composito. *Corymbi* constricti umbelliformes, (2.5–)8–10 cm. longi et lati, ramulis stricte ascendentibus, floribus in sicco pallide flavis. *Pedicelli* in statu fructifero rigidi, divergentes, ascendentes, 2.5–4.5 mm. longi, indumento appresso eo fructuum similiter dense obtecti. *Sepala* 1–1.5 mm. longa, 0.5–0.6 mm. lata, membranacea, cucullata, anguste ovata, obtusa, margine angusta hyalina, pilis stellatis solum 1–7 munita. *Petala* 2–2.5 mm. longa, (0.5–)0.6–0.7 mm. lata, clavata vel obovata, integra vel emarginata, glabra vel raro lamina pilis stellatis munita. *Filamenta longa* 2–2.5 mm. longa, appendicibus 1–1.5-plo longiora; appendix bidentata vel ad apicem minute multidentata, in dimidio inferiore ad filamentum connata, parte libera 0.2–0.3 mm. longa. *Filamenta brevia* 1–1.5 mm. longa; appendix libera filamentum subaequans, apice acuta vel bidentata. *Glandulae* minutae, haud conspicuae. *Antherae* minutae, 0.4–0.5 mm. longae. *Ovarium* obovatum, 1–1.5 mm. longum, 0.5–0.8 mm. latum, sursum apicem

dense piliferorum. *Stylus* in statu florescenti tenuis, glaber, 1.2–1.6 mm. longus, stigmate globoso provisus. *Silicula* uniseminata, elliptica vel anguste obovata, (2–)3–3.5(–4) mm. longa, 1.5–2 mm. lata, pallido-virescens, obtusa vel subacuta, valvis inaequaliter inflatis, indumento parce apicem versus magis conspicuo e pilis stellatis appressis minute punctatis 0.2–0.3(–0.4) mm. diametro 4–8 radiatis multo ramosis composito obsitis. *Ovulum* unum per loculum. *Semina* (0.5–)1–1.5(–2) mm. longa et lata, pallide brunnea, anguste alata, 0.05–0.1 mm. diametro. Fl. June, fr. July.

**Turkey.** C2: Prov. Denizli, Suleymanlar deresi between Acipayam and Abbas Köy, 18 July 1947, *Davis 13461* (BM, E, K); Prov. Burdur, Yeşilova-Denizli, 20 miles from Yeşilova, 900 m., *Quercus* scrub and neglected fields, common in one area, 1 June 1962, *Dudley* (*D. 35324 & 35325*) (A, E). C3: Prov. Antalya, Antalya-Finike, 1350 m., stony ground, flowers yellow, 26 July 1960, *Khan, Prance & Ratcliffe 256* (E, K); dist. Kemer, (Lycia) between Ovacik yayla on Teke Dağ and Boğut yayla near Çalbali Dağ, dominant on metamorphic slopes, 13 July 1949, *Davis 15225* (A, BM, E, K).

The affinity of *Alyssum huber-morathii* with any species occurring in Turkey is difficult to assess. Considering all representatives of sect. ODONTARRHENA, this new species appears most closely allied to *A. fallacinum* Hausskn., a rare species found in Crete and Greek Thessaly. In its habit, *A. huber-morathii* resembles *A. chlorocarpum*, a minor variant of *A. murale* Waldst. & Kit. which occurs in the Pindus region of northern Greece.

The much woodier habit, the very silvery, linear and always conduplicate leaves, and the smaller, usually elliptic fruits with sparser indumentum distinguish *Alyssum huber-morathii* from *A. fallacinum* and *A. murale*. In addition, the new species may be differentiated from *A. fallacinum* by its umbellate fruiting branches and shorter, more fragile pedicels, and from *A. murale* by the slender and often curved styles and very narrow seed-wings. Some affinity is expressed with *Alyssum cypricum* Nyár. which also has conduplicate leaves and, frequently, similar fruits and indumentum. However, *A. cypricum* differs in its smaller spathulate-obovate leaves, usually larger emarginate or truncate fruits with a dense indumentum; larger petals, wingless seeds and a distinctly cushion-forming type of growth.

The populations of *Alyssum huber-morathii* are frequently quite large and show a preference for serpentine or metamorphic rubble, but are distributed over a relatively limited range in southwestern Anatolia.

It is a pleasure to name this distinct species in honor of Dr. A. Huber-Morath, of Basel, Switzerland, a friend and untiring worker on Anatolian Flora, who put his voluminous *Alyssum* collection at my disposal.

**Alyssum pateri** Nyár. subsp. **prostratum** (Nyár.) Dudley, comb. & stat. nov.

*A. prostratum* Boiss. & Huet ex Nyár. Bul. Grăd. Bot. Cluj **18**: 98. *fig. 3, n. 5, fig. 5, n. 4, t. 4, f. 4.* 1938 (!). Holotype, Turkey, B8: Prov. Erzurum,

Armenia, Circa Erzerum, Apr. [sic] June 1853 (Bayburt-Erzurum, Kochapinar, 1829–2134 m.) *Huet s.n.* (JE); isotypes (BM, G, GH, K, W).

*A. divrikii* Nyár. *op. cit.* 93. *fig. 3, n. 6, t. 6, f. 9.* 1938 (!). Holotype, Turkey, B7: Prov. Sivas, Divriki (Divriği), 1000 m., June 1893, *Bornmüller 3247* (JE, non vidi); isotype (G).

*A. erzerumi* Nyár. *op. cit.* 98 — pro syn. (!).

DISTRIBUTION AND HABITAT: Replacing the typical subspecies of central Turkey in the Armenian Highlands and found in disturbed areas, corn fields, gravelly plains, and south-facing igneous and calcareous slopes and screes; alt. 1350–2591 m. Fl. June–July.

This taxon was originally described as a species by Nyárády, but examination of the type material, its duplicates, and additional gatherings shows that it has a maximum of three differential characters which can separate it from *Alyssum pateri*. These are: the wings on the long filament almost as long as the filaments; prominently dentate, retuse petals; and styles with a sparse indumentum. Nyárády himself stated that *A. prostratum* was closely allied to his *A. pateri* subsp. *squarrosoramosum*, now regarded as a synonym of *A. pateri* subsp. *pateri*. Though subspecies *prostratum* replaces the typical subspecies in the Armenian Highlands, their distributions overlap in Turkish Kurdistan. A few intermediates occur in the eastern and southeastern range of the typical subspecies.

Nyárády allies *Alyssum divrikii* to the Iranian *A. lanigerum*; however, the type of indumentum and the flower and fruit morphology of *A. divrikii* indicate that it should be treated as synonymous with *A. pateri* subsp. *prostratum*.

**Alyssum condensatum** Boiss. & Hausskn. subsp. **flexibile** (Nyár.) Dudley, stat. nov.

*A. flexibile* Nyár. Bul. Grăd. Bot. Cluj **7**: 157. *pl. 18, t. 5, f. 122, t. 6, f. 21, t. 7, f. 21, t. 9, f. 33.* 1927(!). **Holotype, Syria.** Circa Zebdaine pr. Damascum, frequens inter saxa jugi, inter Bludam et Halbun, 1896 m., 17 June 1855, *Kotschy 147* (CL, non vidi); isotypes (BM, G, K, W).

*A. alpestre* L. [var.] *β. suffrutescens* Boiss. Fl. Or. 1: 268. 1867 — pro parte quoad plantam a Kotschy lectam (*No. 147*)(!).

*A. surculosum* Shott & Kotschy ex Nyár. *op. cit.* 150. *t. 7, f. 14, t. 9, f. 26*(!). Lectotype, Turkey, C5: Prov. Içel, Bulgar dagh, Gusguta valley (nr. Külek boğ.), 2508 m., 26 June 1853, *Kotschy 10* (W); isolectotypes (G, K).

*A. venustum* Nyár. var. *rosulatum* Nyár. f. *simplex* Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. **1**: 61. 1949(!). Lectotype, Turkey, C5: Prov. Adana, Farasch-Bereketli (nr. Pozanti), 3000 m., July 1909, *Siehe 309* (JE); isolectotypes (BM, E).

*A. condensatum* var. *typicum* Nyár. *op. cit.* 72. *t. 2, f. 3* (!). Holotype, Turkey, B6: Prov. Maraş, Berit dağ, 2338–2743 m., Aug. 1865, *Haussknecht s.n.* (JE); isotype (W).

*A. condensatum* var. *flexibile* (Nyár.) Nyár. *op. cit.* 73 (!).

DISTRIBUTION AND HABITAT: In Anatolia from the Cilician Taurus, Anti-Taurus and rarely in Turkish Kurdistan. Also known from Syria

and Lebanon. A montane and alpine taxon on limestone scree and slopes; often in *Pinus nigra* woods, and mixed *Abies* and *Cedrus* forests; alt. (1400–)2000–3000(–3500) m. Fl. June–July.

The holotype of subsp. *flexibile* (given full specific rank in 1927 and varietal status under *Alyssum condensatum* in 1949 by Nyárády) was referred by Boissier to his polymorphic and indefinable taxon *A. alpestre* L. [var.] *β. suffrutescens*.

The typical expression of subsp. *flexibile* is well distinguished from subsp. *condensatum*, with which it is partially sympatric; but intermediates occur in the area of overlap. The major features differentiating subsp. *flexibile* from the typical subspecies are the wider petals with an indumentum, and the fruits with usually attenuate apex and sparser and easily displaced indumentum.

Subsection **Compressa** Dudley, subsect. nov. TYPE SPECIES: *Alyssum murale* Waldst. & Kit. Pl. Rar. Hung. 1: 5. *t. 6.* 1799 (!).

A subsect. *Inflatis* siliculis compressis vel subinflatis ± undulatis semper conspicue nervosis differt.

Series **Integra** Dudley, ser. nov. TYPE SPECIES: *Alyssum murale* Waldst. & Kit.

Silicula marginibus apteris integris pedicellis rigidis patulis suffulta.

**Alyssum murale** Waldst. & Kit. Pl. Rar. Hung. 1: 5. *t. 6.* 1799. Lectotype, Romania. In muris vetustae arcis Devae in Transylvania atque in rupibus apricis vicini Banatus (PR, *Herb. Waldstein N. 495746a*). (Authentic specimens originally from the Waldstein herbarium are present in the herbaria of BM and GH.)

Due to the extreme polymorphism of *Alyssum murale*, approximately 40 specific and infraspecific epithets have been proposed for minor variations within the taxon which is now designated as subsp. *murale*. The full synonymy of *A. murale* will be published later. When considered throughout the whole morphological distribution pattern, *A. murale* seems to represent one highly variable and actively evolving genetic unit. Within this species, however, there are six reference points of variation which are morphologically and geographically correlated, and merit taxonomic distinction. The following synopsis cites the diagnostic characters and distribution of the recognized infraspecific taxa:

1. Subsp. *murale*: fertile stems few, ascending or lax; stellate hairs on fruits ± dense, 0.2–0.5(–1) mm. diameter; appendages of short filaments always free; seed wings 0.2–1 mm. wide. Widespread in central and southern Europe, the Levant, and extending as far east as Iraq, Caucasia, and Transcaspia.
   a) Var. *murale*: vegetative indumentum bicolorous with equal and ± short-rayed, appressed stellate hairs, 0.2–0.5 mm. diameter; seed wings 0.4–1

mm. wide; leaves flat, midvein on upper surface not conspicuously depressed, uppermost cauline leaves not bracteate or involucrate. Distribution as for subsp. *murale*.

b) Var. *alpinum* Boiss. ex Nyár.: vegetative indumentum and leaves as in var. *murale*; seed wings 0.2–0.3 mm. wide; uppermost cauline leaves bracteate and involucrate. Predominantly Anatolian from the Cilician Taurus to Lazistan and extending into central Caucasus.

c) Var. *pichleri* (Velen.) Dudley: vegetative indumentum bicolorous with stellate hairs 1–1.5 mm. diameter of coarse, long, strigose and unequal rays; seed wings and leaves as in var. *murale*. Forming local populations in Bulgaria, Romania, northern Greece and Yugoslavia.

d) Var. *haradjianii* (Rech. f.) Dudley: vegetative indumentum concolorous with appressed equal-rayed stellate hairs, 0.2–0.5 mm. diameter; seed wings as in var. *murale*; leaves frequently conduplicate, midvein on upper surface conspicuously depressed, uppermost cauline leaves not bracteate or involucrate. The Amanus in southern Anatolia, Syria and Lebanon.

2. Subsp. *stojanoffii* (Nyár.) Dudley: fertile stems many, decumbent or deflexed; stellate hairs on fruits sparse 0.2 mm. diameter; appendages of short filaments always adnate to filament; seed wings ca. 0.2 mm. in diameter or less. Rare on the Greek island of Samothrace and in the southern Rhodope Mountains of Bulgaria.

### Var. pichleri (Velen.) Dudley, stat. nov.

*A. pichleri* Velen. Fl. Bulg. 38. 1891 (!). Holotype, Bulgaria. In collibus ad Philippoplin (Plovdiv), 1890, *Pichler s.n.* (PRC).

DISTRIBUTION AND HABITAT: Rare on calcareous and siliceous substrates in Yugoslavia, northern Greece, Bulgaria, Romania and (?) Turkey-in-Europe; alt. (120–)400–900 m. Fl. May–July. A number of specimens collected from the Dalmatian coast in Yugoslavia are intermediate between var. *pichleri* and var. *murale* in regard to the size and form of the stellate hairs.

Recognition of this taxon at specific, or even subspecific rank, cannot be recommended, because its larger stellate hairs (with unequal and divergent rays) is the only character (cf. Nyárády, 1927, p. 84) which will distinguish it from the typical expression of *Alyssum murale*. The stability of the configuration of its stellate hairs throughout the rather limited range of its distribution (excluding Yugoslavia) make it seem advisable to assign varietal status to *A. pichleri*, rather than to recognize it at any other rank.

### Var. haradjianii (Rech. f.) Dudley, comb. & stat. nov.

*A. haradjianii* Rech. f. Ark. Bot. II. **5:** 172. 1959 (!). Holotype, Turkey. D6: Prov. Hatay: Cassius (Akra dağ) 300–700 m., June 1909, *Haradjian 3021* (G); isotypes (E, K, W).

*A. constellatum* sensu Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. **1:** 96. 1949 — non Boissier!

The characters of *Alyssum haradjianii* by which it may be separated from the typical variety of *A. murale* are not of an order indicating taxonomic distinctness beyond the rank of variety. The height of the fertile stems of the Haradjian gatherings, which caused Rechinger (1959) to interpret this taxon as intermediate between Nyárády's artificial categories "*Humiliories*" and "*Elatiories*," is not constant in the other specimens of the variety. The plants may be as tall or taller than many collections of var. *murale*. The small local populations of var. *haradjianii* are sympatric with var. *murale* in the Amanus of southern Turkey and in montane Syria and Lebanon. However, the concolorous and frequently conduplicate leaves, which always have conspicuously depressed mid-veins, of var. *haradjianii* permit it to be separated from var. *murale*.

Subsp. **stojanoffii** (Nyár.) Dudley, comb. nov.

*A. pichleri* subsp. *stojanoffii* Nyár. Repert. Sp. Nov. **27**: 395. *t. 103, f. 3.* 1930. Holotype, Bulgaria. Macedonia bulgarica, in graminosis alpinis sub cacumine Kalabak, m. Belasica, alt. c. 2000 m., 20 July 1920, *Stojanoff s.n.* (SOM, non vidi).

*A. degenianum* Nyár. Bul. Grăd. Bot. Cluj **7**: 87. *t. 3, f. 45, 46.* 1927 (!). Holotype, Greece. Samothrake, Monte Phenogari, 28 June 1890, *Degen s.n.* (W).

*A. degenianum* f. *subcaespitosum* Nyár. *loc. cit.*(!). Holotype, Greece. Samothrake, Monte Phenogari, 28 June 1890, *Degen s.n.* (W).

DISTRIBUTION AND HABITAT: Montane in grassy meadows on the Greek island of Samothrace and the southern Rhodope Mountains in Bulgaria; alt. (600–)1000–2000 m. Fl. June.

Although the type gathering of this subspecies has not been seen, its original description and accompanying photograph clearly establish it as the same taxon which Nyárády had previously regarded as *Alyssum degenianum*. Additional support for this conclusion is that specimens of *A. degenianum*, determined by Nyárády, have been collected from very near the type locality of subsp. *stojanoffii*. This close proximity and the correlation of the specimens with the literature establishes without much doubt that the two taxa are conspecific. It is evident that because *A. pichleri* differs from *A. murale* only by its very large (1–1.5 mm. in diameter) and coarse stellate hairs, it was necessary to reduce *A. pichleri* to varietal rank. Though subsp. *stojanoffii* was assigned originally to *A. pichleri*, the characters which distinguish it from all the other infraspecific taxa of *A. murale* are of a significance to merit subspecific recognition. Therefore, it would be unrealistic to reduce subsp. *stojanoffii* to the rank of form under var. *pichleri*. The specimens of *A. degenianum* cited by Nyárády (1949) from Lebanon, all refer to *A. murale* var. *haradjianii*.

Subsection **Samarifera** Dudley, subsect. nov. TYPE SPECIES: *Alyssum samariferum* Boiss. & Hausskn. in Boiss. Fl. Or. 1: 272. 1867. Holotype, Turkey, C6: Prov. Maraş, in monte Berytdagh Cataoniae

(Berit dağ), 1829–2338 m., 8 Aug. 1865, *Haussknecht s.n.* (G); isotypes (BM, K, W).

A subsect. *Inflatis* siliculis indehiscentibus samaroideis undulatis pendulis papyraceis semper compressis pedicello capillari flexuoso deflexo suffultis differt.

**Alyssum peltarioides** Boiss. subsp. **virgatiforme** (Nyár.) Dudley, stat. nov.

*A. peltarioides* var. *virgatiforme* Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. 1: 84. 1949 (!). Lectotype, Turkey, B7: Prov. Erzincan, Sipikordagh, 28 July 1890, *Sintenis 3126* (JE); isolectotypes (BM, E, G, K, W).

DISTRIBUTION AND HABITAT: North and central Anatolia, Armenian Highlands, Anti-Taurus and Amanus; on north-facing igneous slopes; alt. 914–2600 m. Fl. June–July.

KEY TO SUBSPECIES

Inflorescence condensed, sparingly branched, not more than 5 cm. long and with 5–15 fruits; stems congested or decumbent 5–10 cm. long. . . . . Subsp. *peltarioides*.

Inflorescence widely spreading, strongly branched, 10–20 cm. long, and with 20–50 (or more) fruits; stems arcuate, ascending or erect, 25–50(–75) cm. long. . . . . Subsp. *virgatiforme*.

The characters distinguishing the infraspecific taxa of this species are constant over its whole range and are coupled with altitudinal and geographical preferences. The most westerly stations of the species are composed entirely of subsp. *virgatiforme*; however, in some localities in the eastern part of the range (Armenia), where the two subspecies are sympatric, they are confined to different altitudes and have different flowering times. The typical subspecies, which flowers later than subsp. *virgatiforme* and has a very reduced habit, is found near melting snow at altitudes from 2000 to 3580 meters. The consistency of their morphological expression in conjunction with the facts of geographical and altitudinal replacement indicates that for these taxa subspecific rank is more realistic than varietal rank.

**Alyssum caricum** Dudley & Huber-Morath, sp. nov. Holotype, Turkey, *Huber-Morath 12824* (HM); isotypes (A, E). PL. II, FIGS. 1–11.

*A. floribundum* Boiss. & Bal. var. *latifolium* Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. 1: 82. 1949 (!). Lectotype, Turkey, *Huber-Morath 5566* (HM).

Affinis *A. peltarioidi* Boiss. et *A. trapeziformi* Bornm. ex Nyár., sed ab ambobus fructibus dissimilibus leviter obcordatis vel late obovatis, stylo longiore tenuiore, habitu magis ramoso, surculis sterilibus crassioribus

fere maioribus differt; insuper a priore fructu minus undulato obscure nervoso et ramulis corymbis longis rigidis ascendentibus minus laxis recedit; a posteriore forma pilorum stellatorum dissimili divergit.

*Frutex* perennis, supra basin multiramosus, basi lignosa efoliata 3–13 cm. alta. *Planta* ex toto (imprimis folia caulium sterilium) indumento albo-argenteo e pilis stellatis radiis (10 -)15–25(–35) undulatis delicatulis longis vel brevibus saepe ramosis composito dense vestita. *Caules floriferi* erecti-ascendentes, e basi parce ramosi, parce foliati, 17–30(–37) cm. alti, basi rubro-purpurei, pilis stellatis appressis multiradiatis superne densioribus tecti. *Surculi steriles* erecti, e parte inferiore caulium floriferorum ascendentes, rare longiores caulibus floriferis (2.5–)5–13 cm. alti (subinde multiramosi et efoliati, ramis 25–30 cm. altis), dense foliati. *Folia caulium floriferorum* anguste oblanceolata vel oblongo-obovata, acuta vel obtusa, 10–15(–20) mm. longa, 1.5–2(–3) mm. lata, petiolis 3–5(–7) mm. longis, in apice bracteis inflorescentiae simulantibus, 7–10(–15) mm. longa, 1–2(–3) mm. lata. *Folia caulium sterilium* bene evoluta bicolora, obovato-oblanceolata, spatulata, basi cuneata, obtusa vel rare subacuta, (7–)10–20 mm. longa, (3–)5–7 mm. lata, petiolis 5–10 mm. longis; pagina superior indumento 3–4-plo minore eo paginae inferioris et radiis paucioribus brevioribus obtecta. *Corymbi* magni, multiramosi, 5–10(–15) cm. alti et lati, ramulis ultimis rigidis stricte ascendentibus 5–10(–15) mm. longis corymbis ultimis umbelliformibus fructibus 4–10(–15). *Pedicelli* fragillimi, tenues, flexuosi, deflexi, (3–)4–5(–5.5) mm. longi pilis stellatis appressis vel subappressis 10–15-radiatis pauce vel dense obsiti. *Sepala* lanceolata vel ovata, acuta, apice cucullata, 2–2.5 mm. longa, (0.5–)0.8–1 mm. lata, margine angusta hyalina et parcis vel copiosis pilis stellatis multiradiatis radiis ± brevibus provisa. *Petala* obovata, spatulata, integra vel subretusa, 3–3.5 mm. longa 1–1.5 mm. lata, glabra vel rare in ungue pilis stellatis paucis provisa. *Filamenta longa* 2.5 3 mm. longa, ala unilaterali in dimidio inferiore connata, apice libero 1–2 dentato 0.3–0.5 (–0.7) mm. longo. *Filamenta brevia* 2 mm. longa, appendice lata libera lanceolata vel oblanceolata acuta vel minute denticulata, (1–)1.5–2(–2.5) mm. longa, 0.4–0.5 mm. lata praedita. *Glandulae* minutae. *Ovarium* 1–1.5 mm. longum, 0.5–1 mm. latum, glabrum, transparens, infime obcordatum, retusum, subflavo-viride. *Stylus* glaber, tenuis, inaequaliter insertus, 1–1.5(–2) mm. longus. *Silicula* uni- vel duoseminata, brunneo-viridia, late obovata vel leviter obcordata, retuse vel rare truncata, basi breve attenuata (5–)6–7.5(–8) mm. longa, 4.5–6(–6.5) mm. lata, saepe pendula, margine parce papillosa imprimis apicem versus, valvis membranaceis glabris laevigatis haud undulatis ad medium subinflatis inconspicue nervosis. *Ovulum* unum per loculum. *Semina* oblonga, compressa, 2.5 mm. longa, 1.5 mm. lata, ala 0.1–0.2(–0.3) mm. lata. Fl. Apr.–June, fr. June–July.

HABITAT: Saxatile on serpentine outcrops, cliffs, ledges and scree; often in *Quercus* scrub and *Pinus brutia* or *P. nigra* woods; alt. (40–)100–900 (–1219) m.

**Turkey.** C2: Prov. Muğla, Muğla-Fethiye, Kalkgeröll linkes Ufer des Namlam Çay, 42 km. südöstlich Muğla, 100 m., 20 June 1954, *Huber-Morath 12824* (HM; A, E); 8 miles s. of Muğla, 590 m., forming dense compact clumps, common in roadside scree and serpentine outcrops, 29 May 1962, *Dudley* (*D. 35132*) (A, E); 25 miles from Muğla, roadside serpentine ledges and scree, 70 m., 29 May 1962, *Dudley* (*D. 35137*) (A, E); Muğla-Marmaris, *Poterium* Macchie, 45 km. südlich Muğla, 20 km. nördlich Marmaris, 40 m., 19 June 1954, *Huber-Morath 12823* (E, HM); 20 km. from Marmaris, 60 m., very dry roadside, and serpentine outcrops, forming dense suffruticose, saxatile, spreading clumps, often leafless up to 2 ft., 5 June 1962, *Dudley* (*D. 35390*) (A, E); Kara böyurtleri Köyu, 30 April 1958, *Kayacik & Yaltirik s.n.* (E); Sandras dağ above Ağla on serpentine, 1219 m., 22 July 1947, *Davis 13563 & 13621* (E); Muğla-Fethiye, rechtes Ufer des Namlam Çay, Macchie, 42 km. südöstlich Muğla, 7 June 1938, *Huber-Morath 5149* (HM); *Pinetum* 116 km. südöstlich Muğla, 6 km. ob. Gölçük, 300 m., 7 June 1938, *Huber-Morath 5566* (HM); Kale Tavas-Muğla, Pinus brutia-Wald, 47 km. nach Kale, 5 June 1938, *Huber-Morath 5567* (HM); Muğla-Kale, 35 km. from Muğla, 900 m., serpentine outcrops in deep gorge, open *Pinus nigra* woods, 28 May 1962, *Dudley* (*D. 35128*) (A, E); 30 km. from Muğla, 850–870 m., steepest descent on road, serpentine outcrops and scree, dominant plant in shade of *Pinus brutia-Pinus nigra* overlap, 28 May 1962, *Dudley* (*D. 35123*) (A, E); 30 miles from Muğla, ca. 25 miles from Kale, 460 m., serpentine outcrops and scree, saxatile on cliffs and ledges, 9 June 1962, *Dudley* (*D. 35531*) (A, E).

*Alyssum caricum* shows the closest affinity with *A. peltarioides* and *A. trapeziforme* Bornm. ex Nyár., from which it is readily distinguished by its distinctive obcordate fruits, shorter styles, extremely woody and branched base (often leafless from the base for a foot or more) and the dense cushion of sterile shoots (often 3–4 feet across).

I have observed that *Alyssum caricum* grows with *A. corsicum* Duby in the lowland areas of Caria, in southwestern Anatolia but is restricted to serpentine outcrops and completely replaces *A. corsicum* in montane and alpine regions. Whereas *A. caricum* has a very restricted distribution of about 100 square miles, *A. corsicum* has a much wider range in western Anatolia and is primarily a plant of neglected fields and disturbed areas.

Nyárády (1949) erroneously described this plant as a variety of *Alyssum floribundum* (var. *latifolium*) to which *A. caricum* is not closely allied, and from which it differs in the shape and indumentum of the leaves and in the strikingly dissimilar fruits. Although a lectotype has been chosen from among the several syntypes of *Alyssum floribundum* var. *latifolium*, it certainly seems more satisfactory to describe this plant as a new species, rather than to apply a *nomen novum*. The description of *A. floribundum* var. *latifolium* is built into the structure of Nyárády's very long key and for this reason lacks the essential details which distinguish *A. caricum* from *A. floribundum* or any other species in subsect. SAMARIFERA. In any event, the epithet *latifolium* could not be applied at the specific level because of the earlier *A. latifolium* Vis., a synonym of *A. minus* (L.) Rothm.

**Alyssum pinifolium** (Nyár.) Dudley, comb. nov.

*Triplopetalum pinifolium* Nyár. Magyar Bot. Lap. **24:** 97. *t. 1, f. 1–14.* 1925 (!). Holotype, Turkey, A1 (A): Prov. Çanakkale, in monte Ulu Dagh prope Renkoi (Erenköy) Anatoliae, 24 Apr. 1883, *Sintenis 292* (LD, non vidi); isotypes (BM, E, G, K, UW, W).

DISTRIBUTION: An Anatolian endemic collected only twice from the Dardanelles.

The decision to treat this taxon, originally described as the type of a monotypic genus, *Triplopetalum* Nyár., as a species of *Alyssum* was difficult. Apart from the problem of assessing the value of the characters used to delimit *Triplopetalum* in a generic sense, the material extant in the numerous herbaria visited consisted only of duplicates of the type collection, all without fruits. Unfortunately, the only other collection (*Kirk*, E), made many years earlier, was also in the flowering state. It is established by overall resemblances and floral morphology, however, that *Triplopetalum* falls within a natural species complex containing all the taxa of sect. ODONTARRHENA with indehiscent fruits and brittle, deflexed or sigmoid pedicels.

The characters distinguishing *Alyssum pinifolium* from the other species of the complex are essentially those which characterized the genus *Triplopetalum*, i.e., the consistent presence of "sphaeroid crystals" appearing as pellucid dots on the sepals, petals, filaments, and ovary; the unusual needle-like, almost cylindrical leaves; and the petals with basal appendages (whence the name of the genus).

That *Alyssum lesbiacum* (Candargy) Rech. f. (1943) possesses consistently appendaged petals, as noted originally by Candargy ("petala . . . unguiculata basi bialata"), cannot be ignored when determining the fate of *Triplopetalum pinifolium*. Without doubt, the petal appendages of *A. lesbiacum* are homologous with those of *Triplopetalum*. The samaroid, indehiscent fruits on fragile sigmoid pedicels of *A. pinifolium* and *A. lesbiacum* clearly ally both to such species as *A. samariferum* Boiss. & Hausskn., *A. peltarioides*, *A. dubertretii* Gomb., etc. To consider *Triplopetalum* as a distinct genus would defeat the purposes of the natural grouping of species within sect. ODONTARRHENA and would cause it to be separated from those species with which it is very closely allied. Furthermore, it would be equally unwarranted to regard *A. lesbiacum* as a species of *Triplopetalum*, thereby also cleaving it from its closest allies.

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## EXPLANATION OF PLATES

### PLATE I

FIGS. 1–13. *Alyssum blepharocarpum*: 1, silicle (side view), × 6; 2–5, silicles showing variability of indumentum (face view), × 6; 6, seed, × 6; 7, sepals, × 9; 8, long filaments, × 9; 9, short filaments, × 9; 10, petal, × 9; 11 & 12,

leaves of two different gatherings, × 2; 13, stellate hairs from upper surface of a leaf, × 40.

FIGS. 14–22. *A. davisianum*: 14, silicle (face view), × 6; 15, silicle (side view), × 6; 16, long filaments, × 9; 17, short filaments, × 9; 18, petal, × 9; 19, sepal, × 9; 20, cauline leaf, × 2; 21, stellate hairs from upper surface of a cauline leaf, × 40; 22, woody base of plant with a sterile shoot, × 1.

## PLATE II

FIGS. 1–11. *A. caricum*: 1, ultimate inflorescence, × 1; 2, silicle (face view), × 6; 3, silicle (side view), × 6; 4, seed, × 6; 5, long filaments, × 9; 6, short filaments, × 9; 7, petal, × 9; 8, sepals, × 9; leaf of sterile shoot, × 2; 10, cauline leaf, × 2; 11, stellate hair from upper surface of a cauline leaf, × 40.

FIGS. 12–22. *A. trichocarpum*: 12, silicle (face view), × 6; 13, silicle (side view), × 6; 14, stellate hair from silicle, × 40; 15, tuberculate hairs from silicles, × 12; 16, seed, × 6; 17, long filaments, × 9; 18, short filaments, × 9; 19, petal, × 9; 20, sepal, × 9; 21, leaf, × 2; 22, stellate hairs from upper surface of a leaf, × 40.

## PLATE III

FIGS. 1–11. *Alyssum corningii*: 1, silicle (face view), × 6.5; 2, silicle (side view), × 6.5; 3, seed, × 6.5; 4, short filament, × 6.5; 5, long filament, × 6.5; 6, petals, × 8; 7, ventral view of outer sepal, × 8; 8, dorsal view of inner sepal, × 8; 9, stellate hair from upper surface of a cauline leaf, × 100; 10, stellate hair from silicle, × 100; 11, stellate hair from lower stem, × 100.

FIGS. 12–20. *A. niveum*: 12, sepals, × 6.5; 12a, detail of base of sepals showing interdigitating hairs, × 26; 13, short filament, × 6.5; 14, long filament, × 6.5; 15, petal, × 8; 16, young ovary, × 6.5; 17, stigma, × 33; 18, cauline leaf, × 4.5; 19, lepidote hair from upper surface of cauline leaf, × 65; 20, lepidote hair from dorsal surface of sepal, × 65.

## PLATE IV

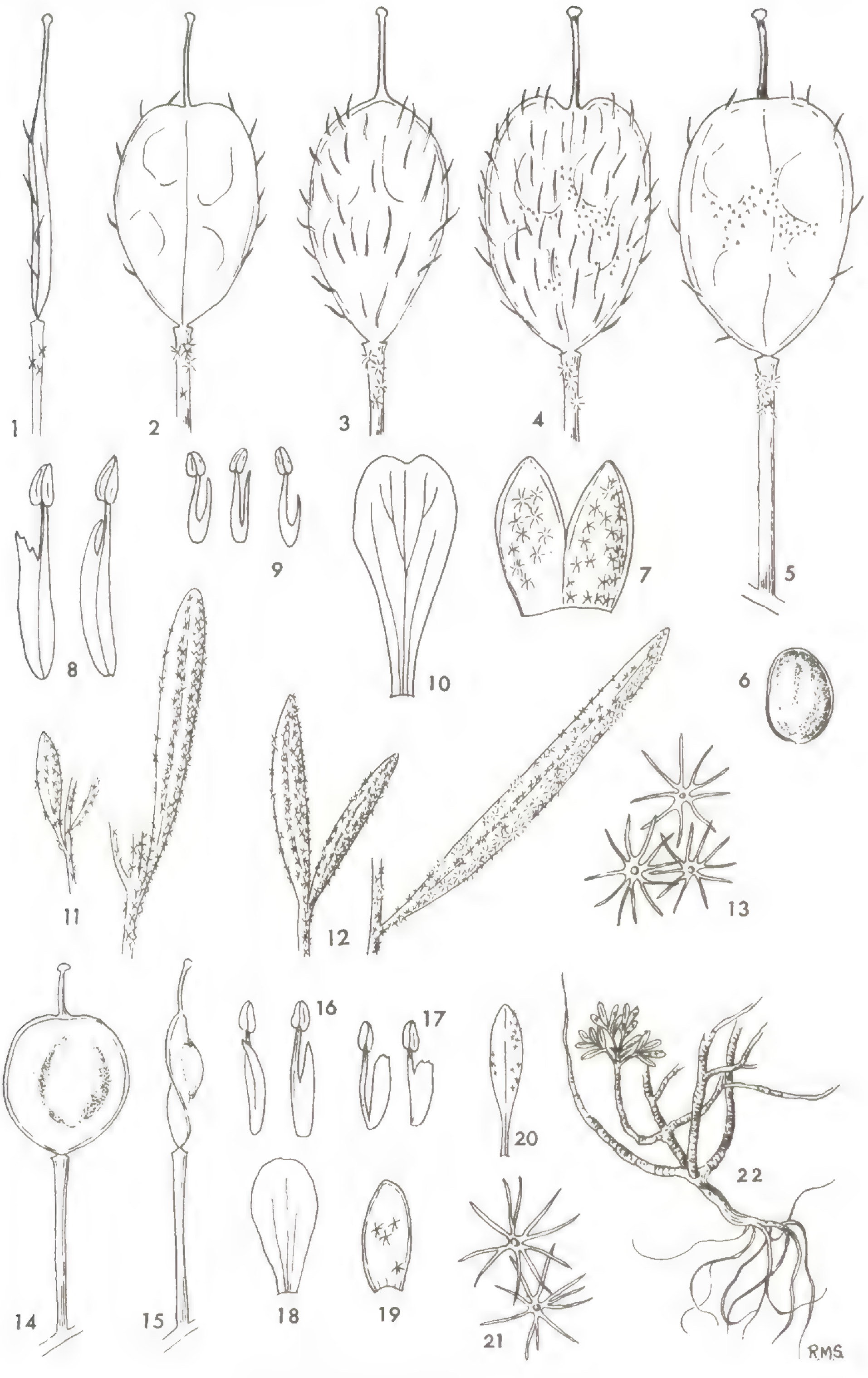
FIGS. 1–12. *Alyssum harputicum*: 1, silicle (immature), × 9; 2, lepidote hair from silicle, × 40; 3, short filament, × 9; 4, long filaments, × 9; 5, petal, × 9; 6, sepals, × 9; 7, ventral surface of a sepal with stellate hairs, × 9; 8, stigma, × 16; 9, sterile shoot, × 2; 10, lower cauline leaves, × 2; 11, upper cauline leaf, × 2; 12, lepidote hair from upper surface of a lower cauline leaf, × 40.

FIGS. 13–26. *A. sulphureum*: 13, ultimate inflorescence, × 1; 14, silicle (face view), × 6; 15, silicle (side view), × 6; 16, stellate hair from silicle, × 40; 17, short filaments, × 9; 18, long filaments, × 9; 19, petal, × 9; 20, sepals, × 9; 21, ventral surface of a sepal with stellate hairs, × 9; 22, tuberculate and divergent rayed stellate hair from apex of a sepal, × 40; 23, sublepidote stellate hair from exterior of a sepal, × 40; 24, seed, × 6; 25, sterile shoot, × 2; 26, cauline leaf, × 2.

## PLATE V

FIGS. 1–11. *Alyssum discolor*: 1 & 2, silicles (face views), × 7; 3, silicle (side view), × 7; 4, sepal, × 9; 5, petals, × 9; 6, long filament, × 8; 7, short filaments, × 12; 8, cauline leaf (lower surface), × 2; 9, leaf of a sterile shoot (upper surface), × 3; 10, stellate hair from upper surface of a cauline leaf, × 95; 11, seed, × 26.

FIGS. 12–23. *A. huber-morathii*: 12, sepals, × 14; 13, short filaments, × 16; 14, long filaments, × 10; 15, silicle (face view), × 9; 16, silicle (side view), × 9; 17, petals, × 10; 18 & 18a, stellate hairs from silicle, × 40; 19, largest leaf of a sterile shoot, × 2; 20, medium leaf of a sterile shoot, × 2; 21, smallest leaf of a sterile shoot, × 2; 22, stellate hair from upper surface of a leaf of a sterile shoot, × 20; 23, seed, × 26.

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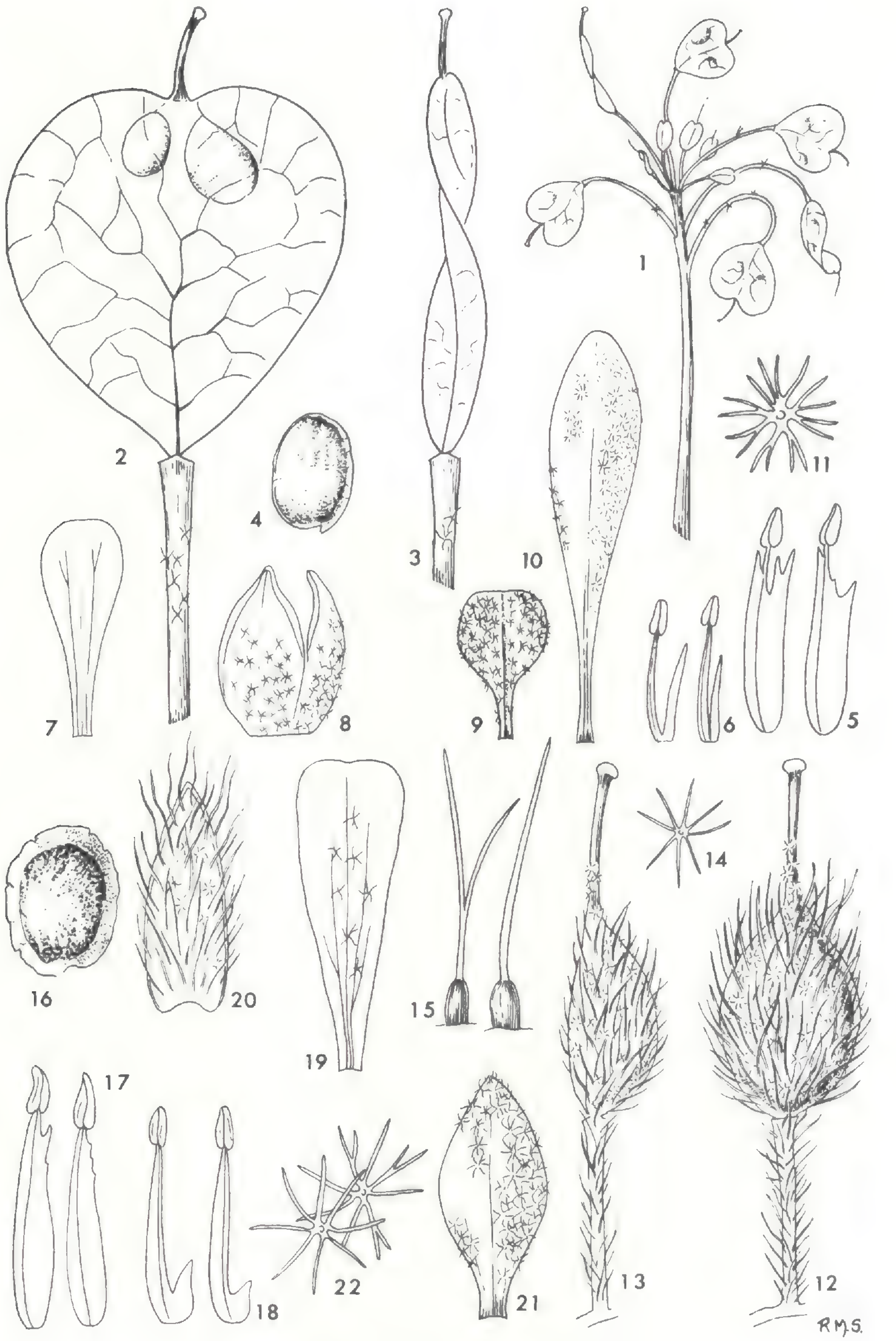


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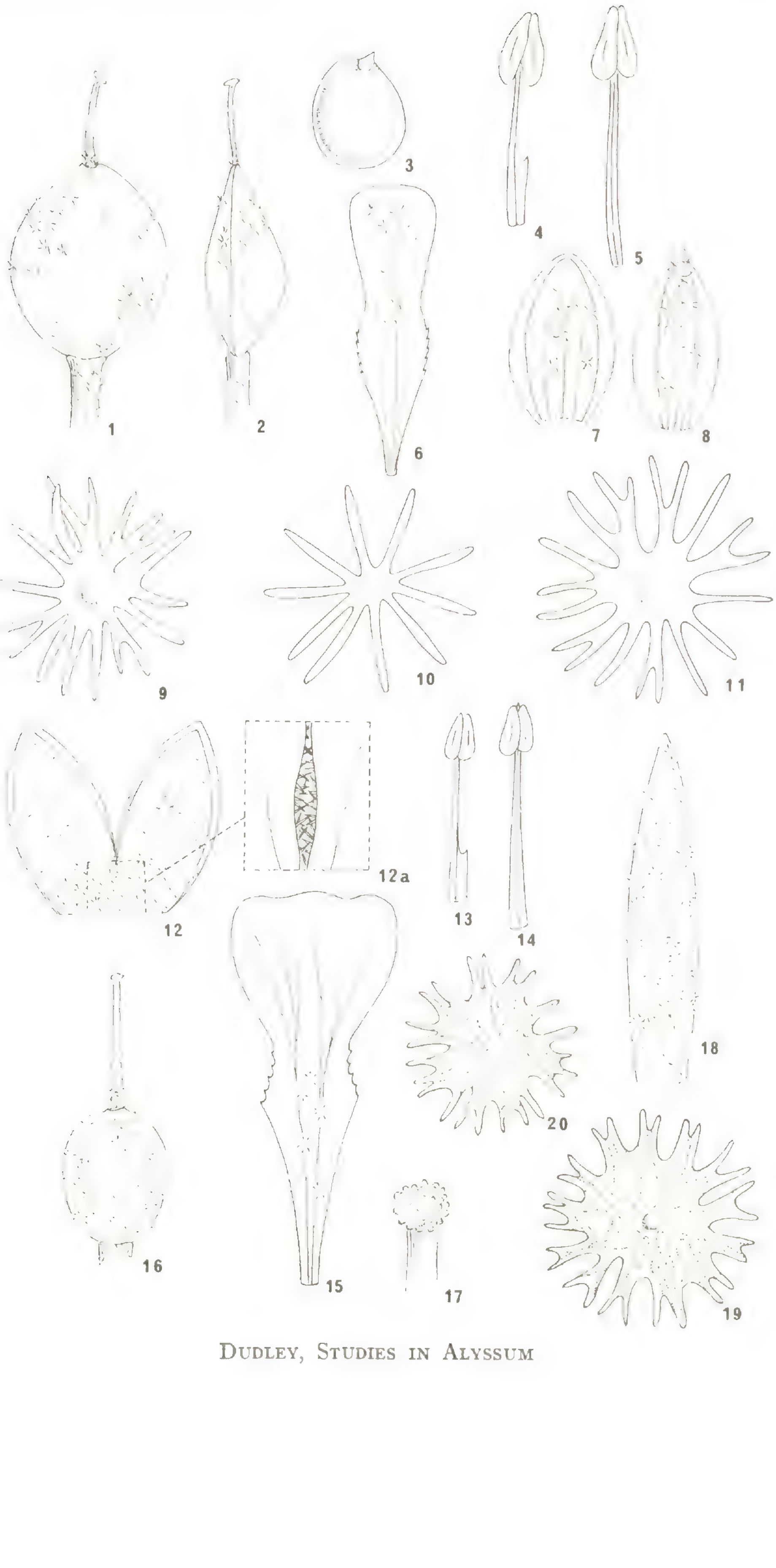


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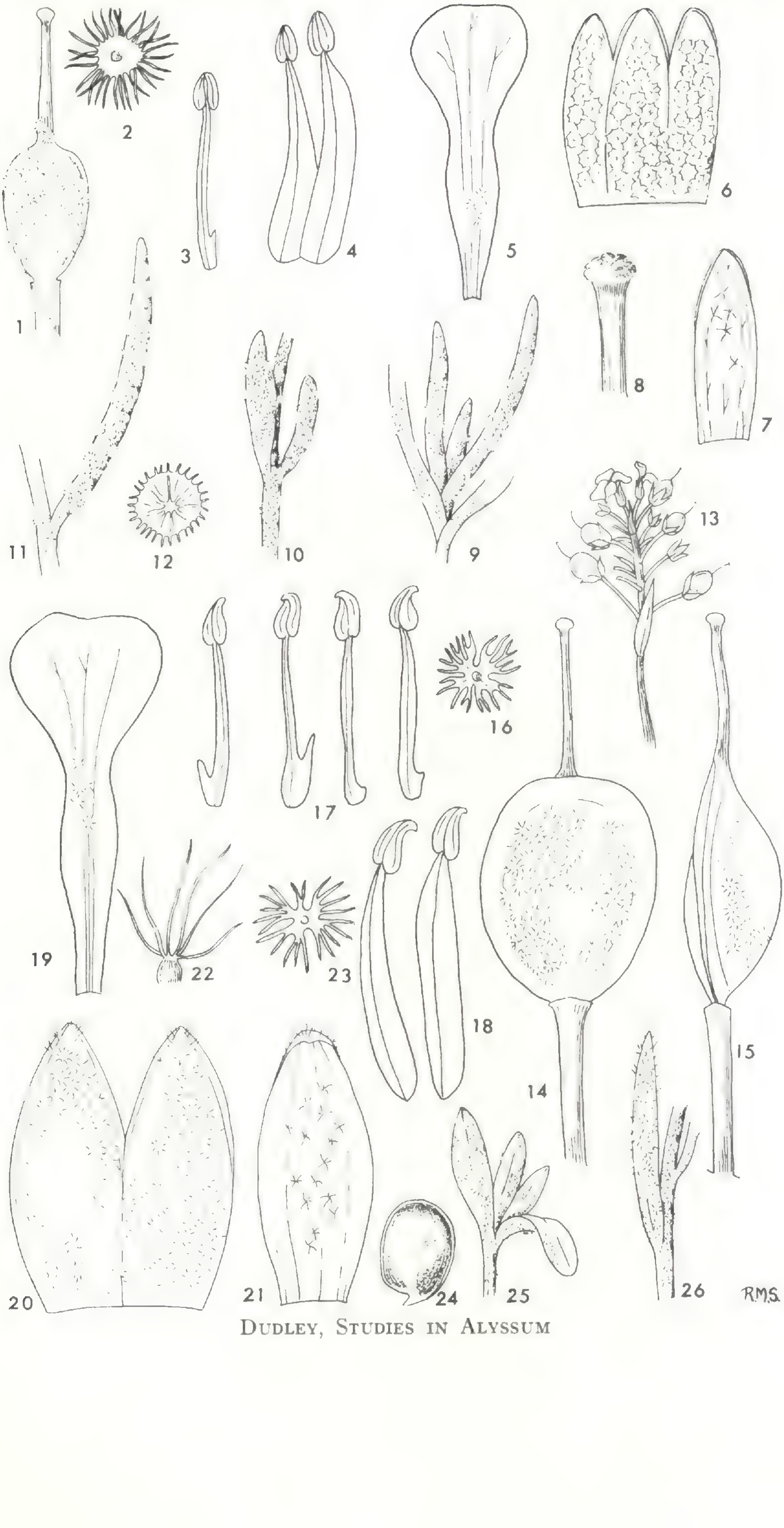


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# THE RUBIACEOUS GENUS MUSSAENDA: THE SPECIES OF THE PHILIPPINE ISLANDS

Don M. A. Jayaweera

In previous papers [1] the morphology of the rubiaceous genus *Mussaenda* has been discussed, and the species of India and Ceylon have been treated. In the Philippine Islands *Mussaenda* is represented by a larger number of species than in the areas considered earlier. Many of the Philippine species are endemic to a single island or are of very limited distribution; only a few may be found throughout the island chain. The Philippine species seem to have some affinity with those of the mainland of China and of the Malayan Peninsula, and to differ rather remarkably from the species of India in the pubescence characters of the inner surface of the corolla tube.

Students of any group of Philippine flowering plants are hampered in their work by the unfortunate loss of the types during World War II. In most cases isotypes are available in one or more of the herbaria of the United States. In such instances a lectotype has been chosen from among them. In some cases it has, however, been necessary to choose a neotype to represent the species.

The institutions from which material has been borrowed for my use were cited in the first of these papers. I should like to express again my appreciation to the officers in charge of these collections for their courtesy, and to the members of the staff of the Arnold Arboretum who have made publication of these studies possible.

The interrelationships of the Philippine species of *Mussaenda* are so complex that an arrangement by affinities seems impracticable at present. For convenience the key which follows is an artificial one. The species have been arranged in alphabetical order.

## ARTIFICIAL KEY TO THE SPECIES OF MUSSAENDA IN THE PHILIPPINE ISLANDS

A. Calyx lobes deciduous almost immediately after flowering.
  B. Stipules entire or faintly bifid at apex.
    C. Corolla tube less than 2 cm. in length.
      D. Corolla tube campanulate, 1.1–1.3 cm. long, corolla lobes broader than long; calyx lobes lanceolate, 5.5–6.5 mm. long, hairy on both surfaces; berry ovoid, 1.2–1.7 cm. long, scantily pubescent; seeds

[1] The rubiaceous genus *Mussaenda*: Morphology of the Asiatic species. Jour. Arn. Arb. **44**: 111–126. 1963. The rubiaceous genus *Mussaenda*: The species of India and Ceylon. *Ibid*. 232–267.

0.43–0.56 mm. long with 3–6 foveae in the areoles of the testa. . . . . 8. *M. lanata.*

D. Corolla tube tubular, broader at the top, 1.7–2 cm. long, corolla lobes broadly ovate, as broad as long; calyx lobes 6–12 mm. long, lanceolate, glabrous or pubescent within; berry (immature) obovoid, 1 cm. long, glabrescent; seeds 0.7–0.83 mm. long with 4–12 foveae in the areoles of the testa. . . . . 6. *M. chlorantha.*

C. Corolla tube 2–3 cm. long, glabrous or straggly pubescent; stipules 7.5–16 mm. long; calyx lobes narrowly oblong-lanceolate or linear, 3.5–6 mm. long, gradually tapering to a point; berry ellipsoid, 1.2–2.2 cm. long, sparsely pubescent; seeds 0.5–0.67 mm. long with 3–6 or 4–12 foveae in the areoles of the testa. . . . . 10. *M. magallanensis.*

B. Stipules bifurcate from the apex for about ½ their length.

E. Midrib of the leaf sunken on the upper surface.

F. Calyx lobes 3–5 mm. long, setaceously pointed; corolla tube slenderly tubular, lobes elliptic, glabrous on the outer surface; stipules broadly lanceolate, 9–12 mm. long; berry ellipsoid, reddish strigose-pubescent; seeds 0.6–0.7 mm. long, with 2–4(–6) foveae in the areoles of the testa. . . . 11. *M. milleri.*

F. Calyx lobes 11–16.5 mm. long, linear with a prominent midvein; corolla tube subfalcate, lobes ovate-lanceolate, granular on the inner surface; stipules ovate-acuminate, 4–5.5 mm. long; berry ellipsoid or globular, 1 cm. long, glabrous, seeds 0.46–0.6 mm. long, with 4–12 foveae in the areoles of the testa. . . . . 13. *M. nervosa.*

E. Midrib of the leaf not sunken on the upper surface.

G. Fruits with persistent, conical, nectariferous discs, nearly glabrous, without lenticels; leaves oblanceolate, 7–20 cm. long, recurved at the apex and decurrently attenuate at base; stipules deciduous, 5–11 mm. long, hairy on both surfaces; calyx lobes lanceolate, 3 mm. long; corolla tube 2.7–4 cm. long; berry ellipsoidally elongated, 1.2–2 cm. long; seeds 0.64–0.77 mm. long, with 3–6(–9) foveae in the areoles of the testa. . . . . 4. *M. attenuifolia.*

G. Fruits without persistent, conical, nectariferous discs.

H. Corolla tube hairy within ⅘ way down, slender, 2–2.5 cm. long; leaves ovate-elliptic, 6–13.3 cm. long; stipules 7–8 mm. long, hairy on the inner surface; calyx lobes linear-oblong, 3.5–5.5 mm. long, sharply acuminate; berry ellipsoid, 1–1.3 cm. long; seeds spiny, 0.83–0.9 mm. long, with 3–9 foveae in the areoles of the testa. . . . . 18. *M. scandens.*

H. Corolla tube hairy within ¼–½ way down.

I. Flower buds curved and club shaped; leaves 9–25.5 cm. long, ferruginous-hairy on both surfaces; stipules 6.5–10.5 mm. long, glabrous on the inner surface; corolla tube 2.2–3 cm. long, hirsute with spreading hairs; berry ellipsoid, 1.5–2.2 cm. long, ferruginous-pubescent; seeds 0.53–0.73 mm. long, with 3–8 foveae in the areoles of the testa. . . . . 20. *M. vidalii.*

I. Flower buds neither curved nor club shaped.

J. Corolla lobes 10–10.5 mm. long, linear-lanceolate, corolla tube very slender, 2.6–3.6 cm. long, pubescent with short,

scattered hairs; leaves 11.5–29 cm. long, pubescent on both surfaces with long, scattered hairs; stipules entire or faintly bifid ⅓ their length, hairy on both surfaces; berry (immature) obovoid, 1–1.3 cm. long; seeds 0.67–0.83 mm. long, with 2–8 foveae in the areoles of the testa. ..... 2. *M. albiflora.*

J. Corolla lobes less than 10 mm. long.

K. Leaves glabrous on the upper surface, minutely pubescent or hirsute beneath, recurved and strongly conduplicate, 3.5–23.5 cm. long; stipules 3–10.5 mm. long; calyx lobes 1.2–7.5 mm. long; corolla tube 2–3.5 cm. long, minutely appressed pubescent; berry globular, 1–1.6 cm. long, lenticellate; seeds 0.6–1 mm. long. with 2–5(–7) foveae in the areoles of the testa. ..... 15. *M. philippica.*

K. Leaves pubescent on both surfaces.

L. Calyx lobes linear, 6–15 mm. long, hairy; leaves 8.5–30 cm. long, long decurrent on petiole from the base; stipules ovate, 9–17 mm. long; corolla tube 2.5–3 cm. long, hirsute, hairs spreading; berry ellipsoid, 1.4–2 cm. long, scantily pubescent; seeds 0.63–0.73 mm. long, with 2–6 foveae in the areoles of the testa. ..... 3. *M. anisophylla.*

L. Calyx lobes lanceolate or oblong-lanceolate.

M. Corolla tube infundibuliform, 2–2.2 cm. long, hairs appressed on the outer surface, lobes acuminate; stipules lanceolate, bifurcate from apex more than ½ their length; calyx lobes 6.7–10.5 mm. long, slenderly acuminate; berry ovoid or obovoid, 1.2–1.4 cm. long, pubescent; seeds 0.6–0.77 mm. long, with 3–6(–8) foveae in the areoles of the testa. ..... 14. *M. palawanensis.*

M. Corolla tube tubular, 2–3 cm. long, hairs horizontally spreading on the outer surface, lobes apiculate; stipules triangular-ovate, bifurcate from the apex for ½ their length; calyx lobes 3.2–8 mm. long, acute; berry globose with very large nectariferous scars; seeds 0.67–0.87 mm. long, with 2–6 foveae in the areoles of the testa. ..... 9. *M. macrophylla* var. *brevipilosa.*

A. Calyx lobes persistent on the ovary after flowering.

N. Inflorescence at the same level or below the terminal leaves.

O. Corolla tube glabrous within, 2.9 cm. long, densely hirsute on the outer surface; calyx lobes short, 1.2–2.5 mm. long, lanceolate; leaves 16–32 cm. long, pubescent on both surfaces; stipules small, slenderly acuminate, bifurcate at the apex, hairy on both surfaces; berry ellipsoid, 1 cm. long, pubescent; seeds 0.64–0.77 mm. long, with 1–4 foveae in the areoles of the testa. ..... 7. *M. grandifolia.*

O. Corolla tube hairy within.

P. Stipules entire or faintly bifid at apex.
Q. Calyx lobes 7.7–8 mm. long, linear-subulate; leaves small, 4–8.3 cm. long, glabrous except on veins beneath; stipules lanceolate, 5–8.5 mm. long, faintly bifid at apex, hairy on the outer surface, hairy within at base and apex only; corolla tube 2–3 cm. long, hairy on the outer surface except at the base; berry not seen. 17. *M. pinatubensis.*
Q. Calyx lobes 10.5–15 mm. long, narrowly lanceolate; leaves 9.5–20 cm. long, glabrate on upper surface, hirsute beneath; stipules 9–13 mm. long, hairy on both surfaces, entire or faintly bifid at apex; corolla tube 2–2.5 cm. long, hairy; berry elliptic, 1.3–1.5 cm. long, rugose; seeds 0.6–0.67 mm. long, with 3–8 foveae in the areoles of the testa. . . . . 16. *M. philippinensis.*
P. Stipules bifurcate from apex for ½ their length, 7–10 mm. long, oblong-ovate; leaves pubescent on both surfaces, 5–15 cm. long; calyx lobes 5–9.5 mm. long, linear-acuminate, gradually tapering to an acute apex; corolla tube 2.7–3.6 cm. long, hairy; berry ellipsoid-fusiform, 1.5–2.5 cm. long, strigose, with calyx segments subpersistent; seeds 0.7–0.77 mm. long, with 4–6(–8) foveae in the areoles of the testa. . . . . 5. *M. benguetensis.*
N. Inflorescence extending beyond the terminal leaves.
R. Leaves with 15–18 pairs of lateral veins, 12–25 cm. long, strigose on both surfaces; stipules ovate, 6–8 mm. long, bifurcate from apex for about ½ their length; calyx lobes linear-lanceolate, 4–7 mm. long, hairy on both surfaces; corolla tube 3 cm. long, hirsute; berry ellipsoid, 1.5 cm. long, sparingly hirsute. . . . . 19. *M. setosa.*
R. Leaves with less than 15 pairs of lateral veins.
S. Calyx lobes broadly lanceolate, 6.7–28 mm. long, 1–6 mm. broad, hairy; leaves 9.5–30 cm. long, densely hirsute on both surfaces; stipules ovate, 12.5–14 mm. long, bifurcate at apex; corolla tube 2.5–3.3 cm. long, densely hirsute, hairs spreading; berry oblong or elliptic, 1.2–2 cm. long, lenticellate; seeds 0.53–0.67 mm. long, faintly spiny, with 4–11 foveae in the areoles of the testa. . . . . 12. *M. multibracteata.*
S. Calyx lobes linear-lanceolate, 11(–15) mm. long, 1.4 mm. broad, hairy; leaves 9–16 cm. long, villous on both surfaces; stipules oblong, 15 mm. long; corolla tube 2.5 cm. long, ferruginous-villous on the outer surface; berry (immature) obovoid, 1.4–1.5 cm. long, sparingly pubescent; seeds 0.46–0.6 mm. long, with 4–8(–11) foveae in the areoles of the testa. . . . . 1. *M. acuminatissima.*

1. **Mussaenda acuminatissima** Merr. Philip. Jour. Sci. Bot. 17: 436. 1920 (TYPE: *Ramos 33133*); Merrill, Enum. Philip. Fl. Pl. 3: 517. 1923. FIG. 4, o, p, q.

Erect shrub about 3 m. high with reddish-brown, lenticellate, glabrous branches and densely ferruginous-villous branchlets. Leaves ovate, 9–16 cm. long, 5–8.5 cm. broad, subcaudate-acuminate at the apex, abruptly long attenuate at base, decurrent on petiole, villous on both surfaces, more densely so on the midrib and veins of the lower surface, lateral veins 10–12 pairs; petiole 1.3–2 cm. long, villous. Stipules oblong, 15 mm. long, acute

or acuminate, hirsute. Inflorescence a terminal, dichotomously branched, pubescent, many-flowered cyme, primary cyme short, axillary cymes from the terminal pair of leaves longer and extending beyond the leaves; bracts and bracteoles linear-lanceolate, about 7 mm. long, acuminate, hairy on both surfaces. Flowers yellow, on stout, pubescent pedicels shorter than the ovaries. Calyx lobes linear-lanceolate, 11(–15) mm. long, 1.4 mm. broad, hairy on both surfaces with one pair of glands at the base of each; petaloid sepal white, ovate or elliptic-ovate, 4–6 cm. long, acuminate, cuneate at base, pubescent on both surfaces: "petiole" about 1 cm. long, hirsute. Corolla tube 2.5 cm. long, ferruginous-villous on the outer surface, hairs within short (long-styled form), extending as far as the bases of the anthers, below glabrous, not tufted at the mouth; corolla yellow, the lobes ovate, 3.5 mm. long and as broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous above the middle of the tube, 3/5 way up; anthers linear, dorsifixed, introrse, 4.5 mm. long, bifid at the base. Ovary broadly fusiform, 5 mm. long, villous, 2-locular with numerous ovules on axile placentae; style 2 cm. long, stigma lobes 7 mm. long, stout, not protruding beyond the corolla tube. Berry (immature) obovoid, 1.4–1.5 cm. long, sparingly pubescent with persistent calyx segments; seeds (immature) minute, reticulate, irregularly oblong or ovoid, 0.46–0.6 mm. long, 0.43–0.56 mm. broad, with 4–8(–11) foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic on the dry slopes of Mt. Nagapatan in Luzon at an elevation of 700 meters above sea level.

**Philippine Islands.** LUZON: Ilocos Norte, Mt. Nagapatan, *Ramos 33133* (NY–lectotype).

Only the isotype from the New York Botanical Garden was available for examination, and I designate it the lectotype.

This species is closely allied to *Mussaenda philippinensis* in its elongated, persistent sepals but differs from it in the indumentum, leaves, oblong stipules, and larger ovaries. *Mussaenda acuminatissima* is distinguished from the other species by its ovate, villous leaves which are acuminate at base and apex, caudate at the apex, abruptly contracted at the base, and decurrent on the petiole, its oblong stipules, short, terminal, primary cymes, pubescent corolla tube, sparingly pubescent fruits with persistent calyx segments, and its minute seeds with 4–8(–11) foveae in the areoles of the testa.

2. **Mussaenda albiflora** Merr. Philip. Jour. Sci. Bot. **5**: 241. 1910 (TYPE: *Curran 17358*); Merrill, Enum. Philip. Fl. Pl. **3**: 518. 1923. FIG. 1, h, i; FIG. 3, a, b, c, d, e.

Erect shrub 2–5 m. tall with terete branches and densely hirsute branchlets. Leaves ovate, oblong-ovate or lanceolate-elliptic, 11.5–29 cm. long, 5.5–9.5 cm. broad, slenderly acuminate at apex, decurrent-acuminate at base, pubescent on both surfaces with scattered, long, spreading hairs,

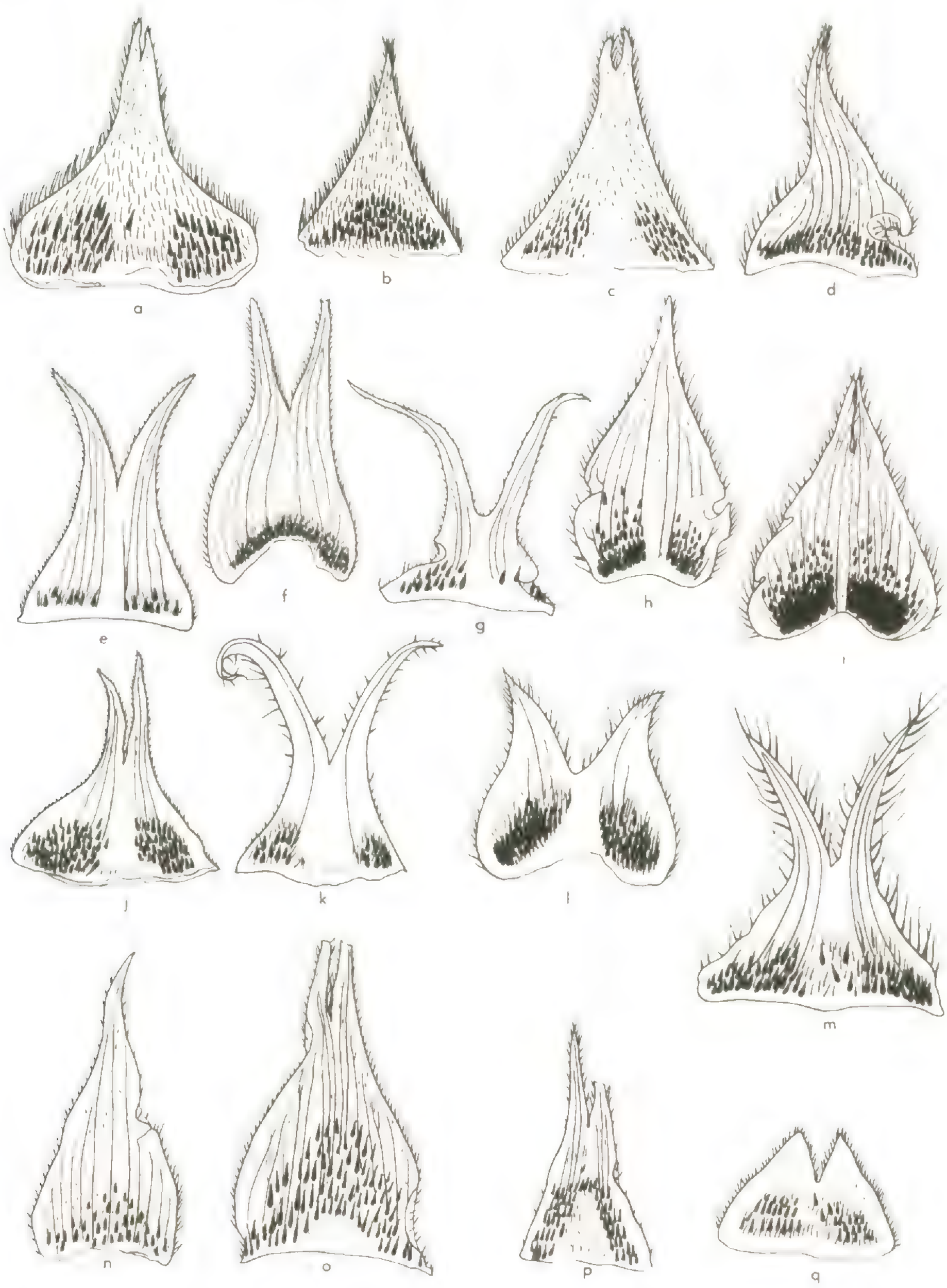


FIG. 1. Stipules of some Philippine species of *Mussaenda* spread out and viewed from the adaxial surface to show bifurcation at the apex and distribution of the hairs and glands. a, *M. lanata* (*Merrill 1768*), × 3. b, c, *M. chlorantha*: b (*Merrill 770*), × 2¾; c (*Elmer 21940*), × 3. d, *M. magallanensis* (*Elmer 12451*), × 3. e, *M. nervosa* (*Ramos & Edano 26422*), × 5. f, *M. attenuifolia* (*Elmer 13304*), × 3¼. g, *M. scandens* (*Elmer 11291*), × 4. h, i, *M. albiflora*: h (*Ramos & Edano 31107*), × 3; i (*Dias 29885*), × 2¾. j, *M. philippica* (*Elmer 7045*), × 4. k, *M. palawanensis* (*Fenix 15531*), × 4. l, *M. benguetensis* (*Santos 5497*), × 3⅓. m, *M. setosa* (*Merrill 9496*), × 4. n–p, *M. philippinensis*: n (*Sulit & Conklin 17652*), × 2½; o (*Escritor 21240*), × 3; p (*McGregor 32449*), × 2¼. q, *M. grandifolia* (*Edano 77424*), × 5, an old stipule, the apical lobes reduced to stumps.

lateral veins 10–14 pairs; petiole 1–3 cm. long, densely hirsute. Stipules broadly ovate or lance-ovate, 1.1 cm. long, 6–7.5 mm. broad at the base, entire or faintly bifid from apex for 1/3 their length, hairy on both surfaces with numerous glands in groups at the base within. Inflorescence a terminal, densely pubescent (with long or short spreading hairs), trichotomously branched, compact cyme; bracts and bracteoles lanceolate, about 7 mm. long, acuminate, hairy on the outer surface, glabrous within. Flowers heterostylous, on stout, pubescent pedicels shorter than the ovaries. Calyx lobes linear-lanceolate, 7–8 mm. long, 0.7–0.9 mm. broad, gradually narrowing to the acuminate apex, hirsute on the outer surface, glabrous within with 2 or 3 pairs of glands at the base of each; petaloid sepal white, ovate to oblong- or elliptic-ovate, 5–7.2(–9) cm. long, 2.7–4.3(–5.5) cm. broad, sharply acute or acuminate at apex, rounded or acute at base, glabrous on both surfaces except on veins beneath, "petiole" 1–2 cm. long, hirsute. Corolla tube white, very slender, 2.6–3.6 cm. long, covered with short, scattered hairs on the outer surface, hairy within as far as the bases of the anthers in long-styled forms, 1/2 way down from the top in short-styled forms, hairs not tufted at the mouth and shorter in long-styled forms; corolla lobes linear-lanceolate, 10–10.5 mm. long, 1.5–2.5 mm. broad, gradually narrowed to an acute apex, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous just below the middle of the tube in long-styled forms and about 2/3 way up from the base in short-styled forms; anthers linear, dorsifixed, introrse, 3.5–4 mm. long, acute at apex, bilobed at the base. Ovary turbinate or cylindric-turbinate, 3–4 mm. long, hairy, 2-locular with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 2 cm. and 6.5 mm. long respectively in long-styled forms, each 3 mm. long in short-styled forms. Berry (immature) obovoid, 1–1.3 cm. long with few, long, scattered hairs, calyx lobes deciduous; seeds minute, reticulate, 0.67–0.83 mm. long, 0.43–0.53 mm. broad, with 2–8 foveae in the areoles of the testa.

ILLUSTRATION. Sulit, Philip. Jour. Forestry 2(1): 43. *pl. 2, fig. 1.* 1939.

DISTRIBUTION. This species grows under humid conditions in gullies to an altitude of about 300 meters above sea level in the islands of Panay and Negros where it is endemic. It has been collected in flower from April to June and in September; in fruit in September.

**Philippine Islands.** NEGROS. *Curran 17358* (NY-lectotype), *17359* (US); Occ. Negros, Iglamgam, *Dias 29885* (A, NY). PANAY: Capiz, Jamindan, *Ramos & Edano 31107* (A), *31382* (US); Libacao, *Martelino & Edano 35391* (A, NY); Antique, *McGregor 32450* (A).

There do not seem to be any close relatives of *Mussaenda albiflora* in the Philippine Islands. It may be distinguished from other species by its large, pubescent leaves; large, ovate or lance-ovate stipules (entire or faintly bifid at the apex); long, slender corolla tubes; linear-lanceolate, white corolla lobes; obovoid, scantily pubescent fruits with deciduous calyx segments; and large seeds with 2 to 8 foveae in the areoles of the testa.

3. **Mussaenda anisophylla** Vidal, Phan. Cuming. Philip. 178. 1885 (TYPE: *Cuming 918*); Merrill, Enum. Philip. Fl. Pl. 3: 518. 1923.

FIG. 3, j–s.

Shrub 2–8 m. high with rather lax, hairy branchlets. Leaves membranous, oblong-ovate or elliptic, 8.5–30 cm. long, 3.2–16 cm. broad, acute or acuminate, cuneate, long decurrent on petioles from the base, hairy on both surfaces with 7–15 pairs of lateral veins; petiole 0.5–5.5 cm. long, stout, hirsute. Stipules ovate, 9–17 mm. long, 4.5–10 mm. broad at the base, bifurcate from apex for about 1/2 their length, lobes straight or diverging, densely hirsute on the outer surface, glabrous within or pubescent with numerous glands in a continuous band. Inflorescence a terminal, di- or trichotomously branched, densely hirsute, diffuse, many-flowered cyme; bracts and bracteoles lanceolate, about 6–9 mm. long, hairy on both surfaces; bracteoles usually in opposite pairs, broader at the base with a few glands and trilaciniate to about the middle, lateral lobes shorter. Flowers heterostylous on stout, densely hairy pedicels shorter than the ovaries. Calyx lobes linear, 6–15 mm. long, 1–2 mm. broad, covered with sharp-pointed, straight, stiff hairs on the outer surface, hairs short within with 2 pairs of glands at the base of each sepal; petaloid sepal white, elliptic-ovate, 7.5–10 cm. long, 3.7–6 cm. broad, acute, cuneate at the base, hirsute on both surfaces, 5-veined, "petiole" 1–2 cm. long, hirsute. Corolla orange to yellow, the tube 2.5–3 cm. long, densely hairy on the outer surface, hairs long and spreading, hairy within as far as the bases of anthers or lower; hairs of the inner surface long in short-styled forms and short in long-styled forms, not tufted at the mouth; corolla lobes broadly ovate, 5 mm. long, 6 mm. broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous about 1/2 way on the tube in long-styled forms and 3/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 5.5–6.5 mm. long, bilobed at the base. Ovary turbinate, 4.5 mm. long, hirsute, 2-locular with numerous ovules on axile placentae; style and stigma lobes 2.2 cm. and 9 mm. long respectively in long-styled forms, 3.5–4 mm. and 2–2.5 mm. long in short-styled forms. Berry ellipsoid, 1.4–2 cm. long, scantily hairy, lenticellate, calyx segments deciduous; seeds minute, reticulate, oblong or orbicular-ovate, 0.63–0.73 mm. long, 0.33–0.63 mm. broad, with 2–6 foveae in the areoles of the testa.

ILLUSTRATION. Sulit, Philip. Jour. Forestry 2(1): 43. *pl. 1.* 1939.

DISTRIBUTION. This species grows near water courses in deeply shaded ravines in the mossy forests at medium elevations up to 800 meters in the islands of Luzon, Alabat, Mindoro, Negros, and Mindanao. It has been collected in flower in January, February, May, June to August, and October; in fruit in February, June, and November.

**Philippine Islands.** LUZON: Albay Prov., *Cuming 918* (BM-lectotype); Pangasinan Prov., Labrador, Mt. San Isidro, *Fenix 29851* (NY, US); Bataan Prov., Mt. Mariveles, Lamao River, *Meyer 3020* (NY, US), *Merrill 2508* (NY, US), *Borromeo 25602* (A, US), Batangas Prov., *Vidal 801* (A); Laguna Prov., Los Banos

(Mt. Maquiling), *Elmer 17481* (A, GH, NY, US); Mt. Makiling, *Canicosa 9730* (PNH), *Sulit 8232* (A, PNH), *7087* (A, PNH); San Antonio, *Ramos 21988* (US), *McGregor 23006* (A, US); Tabayas Prov., Lucban, *Elmer 9154* (A, NY, US); Rizal Prov., Antipolo, *Merrill 1341* (NY); Kalinga Subprov., Balbalan, *Celestino 7819* (A, PNH). ALABAT: *Ramos & Edano 48110* (A, NY, US). MINDORO: Mt. Halcon, *Ramos & Edano 40703* (A), *Edano 3500* (A, PNH); Mt. Ilong, *Edano 3290* (A, PNH). NEGROS: Gimogaan River, *Danao & Aspillera 5218* (US). MINDANAO: Dinagat Island, *Ramos & Convocar 84044* (A).

Probably the only isotypes of this species are in the British Museum (Nat. Hist.) and in the Conservatoire et Jardin botaniques, Genève, since the holotype (*Cuming 918* [PNH]) and other isotypes apparently have been destroyed. The sheet in the British Museum has two specimens of the same species mounted on it. The specimen at the top agrees with the original description and it is therefore selected as the lectotype. This species approaches *Mussaenda magallanensis* in the size and pubescence of its stems, leaves, and inflorescence, but differs from it in the deeply bifurcate stipules, longer calyx lobes, hairy corolla tube, larger stamens, and larger seeds containing fewer foveae in the areoles of the testa. It agrees completely with *Wenzel 442* and *Ramos 15328* from Leyte belonging to *M. magallanensis* in the structure of the seed and the number of foveae in the areoles of the testa. The stipule of *Elmer 17481* resembles typical *M. macrophylla* Wall. except that it is glabrous within.

The species is distinguished by the almost horizontal, long hairs on the stems, leaves, and flowers, the large leaves long decurrent on the petiole, the linear or linear-lanceolate sepals, the large, scarcely pubescent, lenticellate berries with deciduous calyx segments, and the small seeds with 2 to 6 foveae in the areoles of the testa.

USES. The fresh leaves of this species are used medicinally, in the form of a decoction, as a cure for asthma in the Philippine Islands.

4. **Mussaenda attenuifolia** Elmer, Leafl. Philip. Bot. **5**: 1874. 1913 (TYPE: *Elmer 13304*); Merrill, Enum. Philip. Fl. Pl. **3**: 518. 1923.
FIG. 1, f.

Shrub about 5 m. high with grayish-white mottled bark and slender, lax, dark brown, white-lenticellate branchlets, the young suberect portions densely soft ferruginous. Leaves opposite, ascending, submembranous, oblanceolate, 7–20 cm. long, 2–7 cm. broad, abruptly short-pointed, acuinate at the recurved apex, decurrently attenuate at base, sparsely pubescent on the upper surface, more densely soft pubescent along the midrib and veins on the lower surface, veins 10–14 pairs, curved-ascending, obscurely reticulate; petiole 0.5–1.5 cm. long, stout, hirsute. Stipules oblong-ovate, membranous, deciduous, 5–11 mm. long, 4.5–5.5 mm. broad, occasionally split or regularly bifurcate at the apex more than 1/2 way, strigose-hairy on the outer surface, pubescent within with numerous glands in a continuous band at the base. Inflorescence a terminal, pubescent, erect or suberect, dichotomously branched, few-flowered cyme not produced be-

yond the leaves, lower branches curved-ascending, opposite, subtended by slender linear or lanceolate hairy bracts and bracteoles, terminal flowers subsessile. Flowers probably heterostylous on stout, pubescent pedicels shorter than the ovaries. Calyx lobes lanceolate, acuminate or sharply acute, about 3 mm. long, pubescent on both surfaces; petaloid sepal creamy white or white, ovate or elliptic, 8–13 cm. long, abruptly pointed at apex and abruptly attenuate at base, 5-nerved, "petiole" 2–3 cm. long, pubescent. Corolla tube greenish to yellowish-white, 2.7–4 cm. long, pubescent on the outer surface, hairy within as far as the middle of the tube in long-styled forms, hairs short and not tufted at the mouth (short-styled forms not seen); corolla lobes orange to yellow, ovate or more or less oblong, 4 mm. long, 2.5 mm. broad, long-apiculate or acuminate, pubescent on the outer surface, papillate within. Stamens with short filaments, epipetalous a trifle above the middle of the corolla tube; anthers linear, dorsifixed, introrse, 5–5.1 mm. long, slender, blunt at apex, basal sterile portion constricted and bilobed. Ovary turbinate, 3–3.5 mm. long, hairy, 2-locular with numerous ovules on axile placentae; style slender, 1.8 cm. long, stigma lobes flattened, fleshy, 7.5–8 mm. long. Berry ellipsoidally elongate, 1.2–2 cm. long, pubescent when young, becoming nearly glabrous, without lenticels, calyx segments deciduous but the nectariferous disc persistent as a blunt, conical knob; seeds minute, reticulate, blackish brown, 0.64–0.77 mm. long, 0.43–0.63 mm. broad, with 3–6(–9) foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Mindanao where it grows at an elevation of 150 to 450 meters above sea level. Elmer collected it in flower and fruit in July, 1912, and no more recent collections seem to have been made, although he stated that it is "fairly well scattered in wet earth and upon rock ledges of the wooded banks of the Catangan Creek."

**Philippine Islands.** MINDANAO: Agusan Prov., Cabadbaran (Mt. Urdaneta), *Elmer 13304* (A–lectotype; GH, NY, US–isotypes).

Only the isotypes were available for examination. From these the specimen deposited in the herbarium of the Arnold Arboretum is designated as the lectotype. Elmer describes the stipules as "quite variable in size, brown, membranous, deciduous, strigose hairy on the outside, 5 to 8 mm. long, gradually tapering from the expanded base to the setiform apex, occasionally split." The stipule in fact is much longer, 10–11 mm. in length, bifurcate more than 1/2 way from the apex in all examples examined.

This species seems to be allied to *Mussaenda palawanensis*, though it differs much in the form of the leaf, inflorescence, etc. It agrees in the character of the stipule except for its hairiness and the banded glands inside. Other common characters are the deciduous calyx, ovate-acuminate corolla lobes, size of the seed, and foveae in the areoles of the testa. It is distinguished from other species by the obovate-oblong leaves with recurved, abruptly acuminate apices and the decurrent-attenuate bases; deeply bifurcate, oblong-ovate stipules with glands at the base within a continuous band; acuminate-apiculate, ovate corolla lobes; glabrous, ellipsoid berries

(not lenticellate) with a pointed, conical, persistent, nectariferous disc at the apex, and minute seeds with 3–6(–9) foveae in the areoles of the testa.

5. **Mussaenda benguetensis** Elmer, Leafl. Philip. Bot. 1: 13. 1906 (TYPE: *Elmer 5935*); Merrill, Enum. Philip. Fl. Pl. 3: 518. 1923. FIG. 1, l; FIG. 3, x, y, z, aa.

Shrub, sometimes tree-like, 1–4 m. tall with ferruginous-pubescent branches. Leaves clustered toward the ends of branches, ovate, oblong or oblong-lanceolate, 5–15 cm. long, 2.3–5.2 cm. broad, acute or acuminate, abruptly cuneate at base, rounded or decurrent-acuminate, appressed pubescent on both surfaces, scantily on the upper surface, more densely especially on the prominent veins of the lower surface, lateral veins 8–11 pairs, ascending; petiole 0.5–2.5 cm. long, densely hirsute. Stipules subpersistent, broadly oblong-ovate, 7–10 mm. long, 6.8–8 mm. broad, bifurcate from apex for about 1/2 their length, rami gradually tapering and diverging into 2 acuminate lobes, hairy on the outer surface, glabrous within except for a few hairs at the apices of the divergent lobes and at the base between numerous glands occurring in 2 groups. Inflorescence a terminal, subcorymbose cyme barely exceeding the leaves in length, pubescent, ultimate branches terminating in clusters of 3 to 5 flowers; bracts and bracteoles lanceolate, 4–13 mm. long, 0.7–2 mm. broad, pubescent on the outer surface, scantily hairy or glabrous within, bracteoles bifid or trifid, lateral lobes shorter. Flowers heterostylous, fragrant, on stout, pubescent pedicels shorter than the ovaries. Calyx lobes linear-acuminate gradually tapering to an acute apex, 5–9.5 mm. long, pubescent on the outer surface, scantily pubescent or glabrous within with 2 or 3 pairs of glands at the base of each; petaloid sepal whitish, small, ovate or elliptic, 3.8–5.2 cm. long, 2–2.8 cm. broad, scantily pubescent on the upper surface, densely pubescent especially on the veins of the lower surface; "petiole" short, stout, 0.5 cm. long, hirsute. Corolla yellow, the tube 2.7–3.6 cm. long, hairy on the outer surface, hairy within 1/2–5/9 way down from the top in long-styled forms, 1/4–1/3 way in short-styled forms, hairs not tufted at the mouth and shorter in long-styled forms; corolla lobes ovate or suborbicular, 4–5 mm. long, 3.4–6 mm. broad at the base, acute, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous about 1/2 way on the tube in long-styled forms, 2/3–3/4 way up from the base in short-styled forms; anthers linear, dorsifixed, introrse, 5–7 mm. long, bilobed at the base, lobes diverging. Ovary broadly fusiform, 5–6 mm. long, pubescent, 2-locular with numerous ovules on axile placentae; style and stigma lobes 1.75–2.2 cm. and 8.7–12 mm. long respectively in long-styled forms, 4–6 mm. and 3–3.5 mm. long in short-styled forms. Berry ellipsoid-fusiform, 1.5–2.5 cm. long, strigose, lenticellate with subpersistent calyx segments; seeds minute, reticulate, 0.7–0.77 mm. long, 0.53–0.63 mm. broad, with 4–6(–8) foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Luzon and grows on open

slopes and in thickets or ravines from 900 to 2300 meters elevation. Elmer comments in his field notes that the plant grows ". . . in ravines but usually in open places; or skirting dense hardwood jungles of the limestone region at 4500 feet; . . ." It has been collected in flower from January to June, October, and November; in fruit from January to June and in December.

**Philippine Islands.** LUZON: Mountain Prov., Baguio, *Steiner 22585* (PNH), *35835* (PNH, US), *41617* (PNH), *Elmer 5935* (PNH–holotype, NY–isotype), *8431* (A, NY, US), *Williams 1006* (GH, NY, US), *Sulit 7722* (PNH), *Walker 7501* (US), *Topping 64* (US), *Santos 34* (A); Mancayan to Baguio, *Ramos & Edano 40504* (A); Mt. Santo Tomas, *Sinclair & Edano 55365* (PNH), *Quisumbing 2193* (A, PNH), *Garcia 34977* (PNH), *Elmer 6536* (NY, US), *Clemens 51845* (A, US); Barrio Agawa, Besao, *Santos 5497* (US); Mt. Libbing, *Mendoza 40936* (PNH); Mt. Polis, *Steiner 41580* (PNH); Benguet Subprov., Papuai, *Santos 31880* (NY), *32026* (A), *Merrill 713* (US); Bontoc, Mt. Santo Tomas, *Walker 7543* (US); Mt. Polis, *Ramos & Edano 37633* (A); Lepanto Dist., Balili (Mt. Data), *Merrill 4639* (US); Ifugao, Mt. Polis, *McGregor 19779* (US). CULTIVATED: Trinidad, *Loher 1523* (US).

As in the case of *Mussaenda pinatubensis*, the holotype of *M. benguetensis* was not destroyed in World War II.

The collection *Vanoverbergh 190* (A) is interesting, for it possesses the stipules and leaf characters of *Mussaenda lanata* and the floral characters of *M. benguetensis*. Its stipules are triangular-acuminate, 13 mm. long, 7.5 mm. broad, not bifid at the apex, hairy on both sides, with numerous glands at the base within. The corolla tube is 2.5 cm. long, larger than that of *M. lanata* but smaller than in *M. benguetensis*. It was collected in Bontoc Subprovince, Luzon, where the two species overlap.

One sheet of *Williams 1006* bore two abnormal flowers one of which was dissected. It had a calyx and corolla of 10 segments each but 15 stamens and 3 ovaries fused together with 7 stigma lobes. The filaments of the innermost stamens were longer, about 5 mm. in length.

It has been observed that several fruits with mature seeds bore calyx segments while in others the calyx segments have been shed. Elmer refers to the petaloid sepal as a "persistent bract" but does not comment on the other sepals. It is probable that the calyx is subpersistent on the fruit.

*Mussaenda benguetensis* is distinguished from other species by its smaller leaves confined to the ends of branches with prominent veins on the lower surface, oblong-ovate stipules with diverging apical lobes, larger elliptic-fusiform, lenticellate berries with or without calyx segments, and somewhat larger seeds with 4–6(–8) foveae in the areoles of the testa.

6. **Mussaenda chlorantha** Merr. Philip. Jour. Sci. Bot. **8**: 47. 1913 (TYPE: *Merrill 770*); Merrill, Enum. Philip. Fl. Pl. **3**: 518. 1923. FIG. 1, b, c; FIG. 2, d, e.

Tree 6–8 m. tall with glabrous, reddish-brown, lenticellate branches, the younger ones appressed pubescent. Leaves broadly ovate, 9.5–16 cm.

long, 6–9.5 cm. broad, sparsely hirsute on the upper surface, puberulous beneath and appressed hirsute on the midrib and lateral veins, short acuminate at apex, abruptly cuneate and somewhat decurrent at base; lateral veins 7–12 pairs, arcuate; petiole 1–4 cm. long, hirsute. Stipules 8.5–10 mm. long, 4.5–6.5 mm. broad at the base, triangular-ovate or oblong-ovate, entire or bifid at apex, densely hirsute on both surfaces with numerous glands in 2 groups or in a continuous band at the base within. Inflorescence a terminal, hirsute, many-flowered, corymbose cyme; bracts and bracteoles linear-oblong to oblong-lanceolate, 4–7 mm. long, hairy on both surfaces, bracteoles larger, trifid, the lateral lobes reduced to stubs. Flowers on stout, pubescent pedicels shorter than the ovaries. Calyx lobes 6–12 mm. long, 1.2–2.2 mm. broad, lanceolate, acuminate, pubescent on the outer surface, glabrous or pubescent within with 1 or 2 pairs of glands at the base of each; petaloid sepal white, broadly ovate, 5–8 cm. long, glabrous on the upper surface, hairy on veins beneath, "petiole" about 2 cm. long, hirsute. Corolla tube green, 1.7–2 cm. long, hirsute on the outer surface, clothed with short hairs (0.5 mm. long) within for 3/4 the length of the tube, basal 1/4 glabrous, hairs not tufted at the mouth; corolla lobes yellow, broadly ovate, 3–4.5 mm. long, 3.5–4.5 mm. broad, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous 1/2 way or higher up on the tube; sometimes filaments free (for about 2.5 mm.) as short loops midway between the base of the corolla tube and the stamens; anthers linear, dorsifixed, introrse, 3.5–5 mm. long, acute, bifid at base. Ovary oblong-turbinate, 5–6 mm. long, appressed pubescent, 2-locular, with a thick wall and axile placentation; style and stigma lobes 1–1.4 cm. and 5–6.5 mm. long respectively; stigmas stout, linear, diverging, above the anthers or placed at the same level as the anthers and surrounded by them. Berry (immature) obovoid, 1 cm. long, glabrescent, calyx lobes deciduous; seeds minute, reticulate, 0.7–0.83 mm. long, 0.5–0.56 mm. broad with 4–12 foveae in the areoles of the testa.

DISTRIBUTION. This species was collected in flower in May by Merrill and by Elmer in Luzon at an altitude of about 1800 meters; it has not been recollected.

**Philippine Islands.** LUZON: Benguet Subprov., Mt. Tanglon, *Merrill 770* (US–lectotype), May 1911; Pampanga Prov., Camp Stotsenburg (Mt. Pinatubo), *Elmer 21940* (GH, PNH), May 1927; Twin Peaks, *Elmer 6318* (US), May 1904.

Elmer's collections differ slightly from the type in the bifid stipules with glands in two groups at the base within and sepals hairy on both surfaces. Otherwise the collections resemble each other closely. *Mussaenda chlorantha* is allied to *M. macrophylla* Wall. var. *brevipilosa* Jayaweera, particularly *Fenix 3770* (NY, US), but differs in its shorter corolla tube and the position of the stigma lobes.

*Mussaenda chlorantha* is distinguished by its broadly ovate leaves; entire or bifid, densely hirsute, triangular-ovate stipules; oblong-lanceolate sepals; short corolla tube with broadly ovate lobes; large, oblong-turbinate ovary, stout stigma lobes, and 4 to 15 foveae in the areoles of the testa.

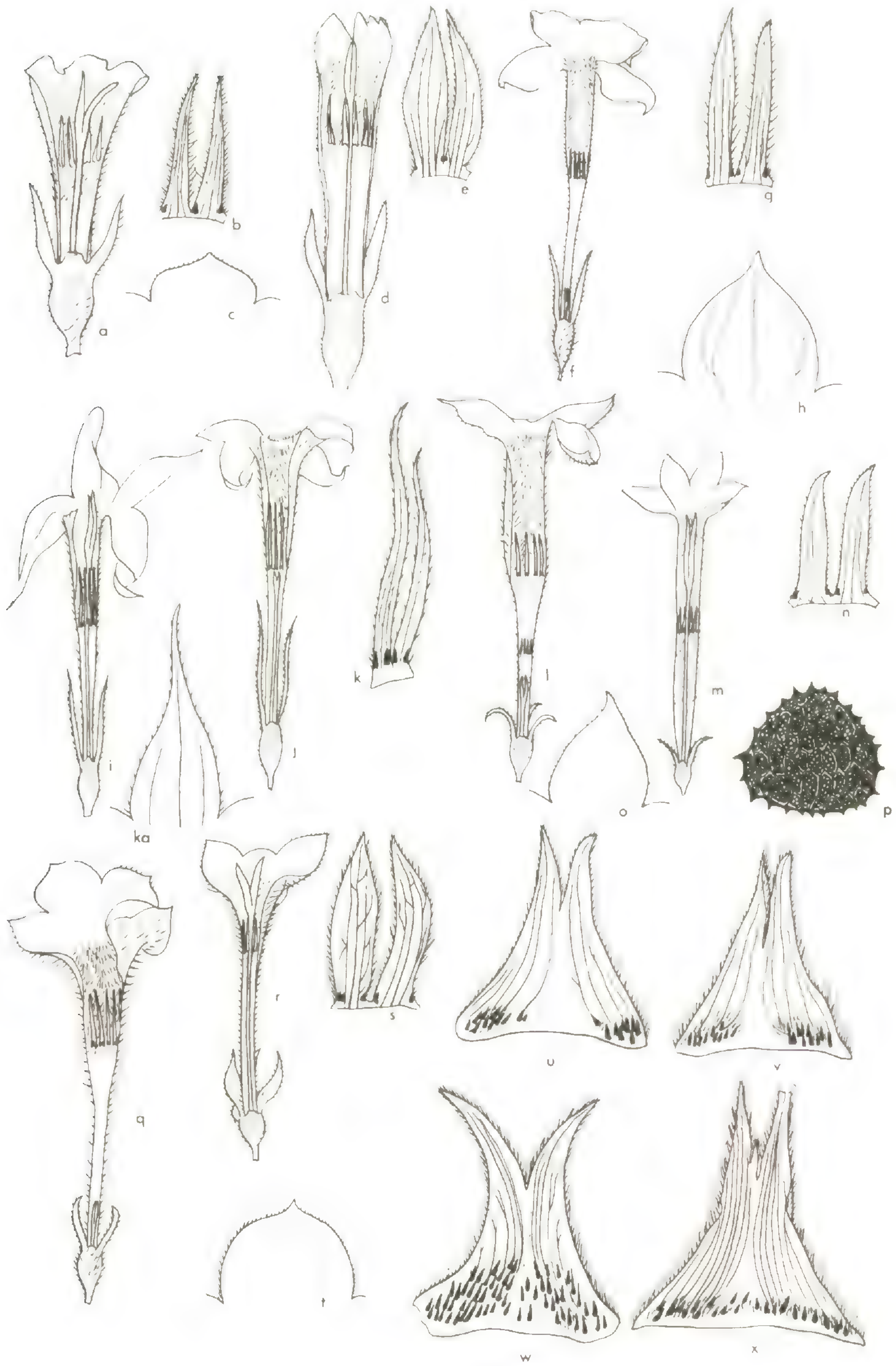


FIG. 2. Longitudinal sections of long-styled and short-styled flowers of some Philippine species of *Mussaenda* with calyx and corolla lobes seen from within, and a seed of *M. scandens*. a–c, *M. lanata*: a (*Merrill 1768*) × 2; b (*idem*), calyx lobes, × 2½; c (*idem*), corolla lobe, × 6. d, e, *M. chlorantha*: d (*Elmer 21940*), × 2; e (*idem*), calyx lobes, × 3. f–h, *M. magallanensis*: f (*Elmer*

7. **Mussaenda grandifolia** Elmer, Leafl. Philip. Bot. 1: 12. 1906 (TYPE: *Merrill 817*); Merrill, Enum. Philip. Fl. Pl. 3: 518. 1923. FIG. 1, q; FIG. 4, a, b, c.

Shrub 3–4 m. high with densely pubescent younger branchlets. Leaves ovate, oblong or oblanceolate, 16–32 cm. long, 7.5–15 cm. broad, acute at apex, cuneate or long attenuate at base, pubescent on both surfaces, densely so beneath and on the 11–14 pairs of lateral veins; petiole 1–2.5 cm. long, villous. Stipules small, slenderly acuminate from a broad base, bifurcate at the apex, hairy on both surfaces with numerous glands in 2 groups or in a continuous band at the base within. Inflorescence terminal, shorter than leaves, pubescent, trichotomously branched, branches straight, divaricate, diffuse, terminal flowers sessile and others subsessile; bracts and bracteoles small, ovate, 1.5–2 mm. long, 0.5–1.5 mm. broad, acuminate, hirsute on both surfaces. Calyx lobes small, lanceolate, 1.2–2.5 mm. long, 0.7–1 mm. broad, acuminate, hairy on both surfaces with 1–3 pairs of glands at the base of each; petaloid sepal yellowish white, broadly ovate, 4.5–7 cm. long, 4–4.5 cm. broad, puberulous on the upper surface and hirsute beneath especially on veins, "petiole" 1 cm. long, hirsute. Corolla yellow, the tube 2.9 cm. long, densely hairy on the outer surface, glabrous within except for a few short hairs in 5 groups at the bases of the corolla lobes; corolla lobes ovate, 4 mm. long, acuminate, hairy on the outer surface. Stamens with short filaments, epipetalous at slightly different levels about 1/2 way on the tube or a little below in the long-styled forms; anthers linear, dorsifixed, introrse, 3.2–4.2 mm. long, of different sizes in the same flower, acute at apex and bifid at the base. Ovary broadly fusiform, 4.5 mm. long, densely hirsute, 2-locular with numerous ovules on axile placentae; style 2.2 cm. long, stigma lobes 1 cm. long and stout in long-styled forms. Berry ellipsoid, 1 cm. long, pubescent with small, persistent calyx segments; seeds (immature) minute, reticulate, 0.64–0.77 mm. long, 0.43–0.53 mm. broad, with 1–4 foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Palawan where it grows in forests at lower elevations. It has been collected in flower and fruit in February and March.

**Philippine Islands.** PALAWAN (Paragua): Point Separacion, *Merrill 817* (US–lectotype); Panalingajan River, *Edano 77424* (A).

Only two collections were available for examination, of which one was

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*12451*), × 1½; g (*idem*), calyx lobes, × 4½; h (*idem*), corolla lobe, × 4½. i–ka, *M. nervosa*: i (*Elmer 10510*), × 2¼; j (*Ramos & Edano 26422*), × 1⅙; k (*idem*), calyx lobes, × 2; ka (*idem*), corolla lobe, × 3. l–p, *M. scandens*: l (*Wenzel 3354*), × 1½; m (*Elmer 11291*), × 1½; n (*idem*), calyx lobes, × 4; o (*idem*), corolla lobe, × 6; p (*idem*), seed, × 23. q–x, *M. vidalii*: q (*Ramos & Edano 39035*), × 1½; r (*Sulit 6098*) × 1; s (*idem*), calyx lobes, × 3; t (*idem*), corolla lobe, × 4; u–x, stipules, u (*Sulit 6280*), × 3½; v (*Elmer 11309*), × 3½; w (*Sulit 6098*), × 3; x (*Ramos & Edano 39035*), × 3¼.

an isotype (which now becomes the lectotype). Both collections were long-styled forms, and heterostyly of the species is not established, though it is quite likely that a short-styled form exists which has not been collected up to now. Elmer's description of the pubescence of the calyx segments and the corolla tube is not accurate. He says that the calyx segments are "glabrous on the inner surface" and the corolla tube "lanose on the interior." An examination of the lectotype specimen shows that the calyx segments are pubescent on the inner surface and the corolla tube glabrous on the interior. The species does not seem to be allied to any of the Philippine mussaendas though it resembles *M. vidalii* in its inflorescence and sessile terminal flowers. It is distinguished from the other species by the large, pubescent leaves; small stipules; sessile terminal flowers in the forks of the peduncles; corolla tube glabrous on the interior surface; pubescent fruits with small, persistent calyx segments; and minute seeds with 1 to 4 foveae in the areoles of the testa.

8. **Mussaenda lanata** C. B. Robinson, Philip. Jour. Sci. Bot. 6: 357. 1911 (TYPE: *Merrill 6681*); Merrill, Enum. Philip. Fl. Pl. 3: 518. 1923. FIG. 1, a; FIG. 2, a, b, c.

Shrub or small tree 2–5 m. high with greenish-gray, pubescent branchlets. Leaves unequal at nodes, ovate, oblong or orbicular, 10.5–30 cm. long, 6.5–16.5 cm. broad, abruptly acute or acuminate at the apex, cuneate at the base, hirsute on both surfaces, more densely so beneath, with 8–13 pairs of lateral veins; petiole 0.8–7.5 cm. long, stout, hairy. Stipules ovate, long acuminate, 10–18.5 mm. long, 6–8.5 mm. broad at the base, faintly bifid at apex, hairy on both surfaces, with numerous glands in 2 groups or in a continuous band at the base within. Inflorescence a terminal, dichotomously branched, densely pubescent, many-flowered, subcorymbose cyme; bracts and bracteoles lanceolate, 3–7 mm. long, hairy on both surfaces. Flowers heterostylous, on stout, densely pubescent pedicels shorter than the ovaries. Calyx lobes lanceolate, 5.5–6.5 mm. long, 1–1.2 mm. broad, acute, hairy on both surfaces, with a pair of thin glands at the base of each lobe; petaloid sepal white, oval, 4.5–5.5 cm. long, 3–3.7 cm. broad, hirsute on both surfaces, 5-veined, "petiole" 1.4 cm. long, hirsute. Corolla tube 1.1–1.3 cm. long, campanulate, yellow-tomentose on the outer surface, hairy within to 1/2 the length of the tube in long-styled forms and 1/3 the length of the tube from the top in short-styled forms, glabrous at base; hairs of the throat long (1.5–1.7 mm.) in short-styled forms and short (1 mm. long) in long-styled forms, not tufted at the mouth; corolla lobes broader than long, somewhat truncate, 1.2–1.5 mm. long, 2.2–3 mm. broad, mucronate or abruptly apiculate at the apex, brown-tomentose on the outer surface, papillate within. Stamens with short filaments epipetalous 3/4 way up on the tube in short-styled forms, (lower down) about 1/2 way up in long-styled forms; anthers linear-lanceolate, dorsifixed, introrse, 3–4 mm. long, acute at the apex, bilobed at the base. Ovary turbinate, 3.5–4.5 mm. long, densely hairy, 2-locular,

with numerous ovules on cushion-shaped, axile placentae, nectariferous disc well developed; style and stigma lobes 5–7 mm. and 5 mm. long respectively on long-styled forms, 1.6 mm. and 1.8 mm. long in short-styled forms. Berry ovoid, with a fruity fragrance, 1.2–1.7 cm. long, scantily pubescent, lenticellate, with deciduous calyx segments; seeds minute, reticulate, angularly rounded, 0.43–0.56 mm. long, 0.36–0.43 mm. broad, with 3–6 foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Luzon and grows in thickets along streams from 900 to 1600 meters elevation. It has been collected in flower in March, April, May, August, October, and December; in fruit in October, November, and December.

**Philippine Islands.** LUZON: Abra, *Ramos 7254* (NY, US); Bontoc, *Ramos & Edano 38134* (A); Benguet, Sablan, *Elmer 6195* (NY, US), *Williams 1558* (GH, NY, US), *Merrill 6681* (US–lectotype); Baguio, *Mabesa 35292* (PNH), *Elmer 8976* (A, NY, US), *Curran 5078* (US); Sabang, *Fenix 12588* (US); Itogon, *Williams 1011* (GH, NY, US), *Merrill 1768* (GH, NY), *Loher 1524* (US), *Clemens 17249* (NY); Ilocos Spur, Mt. Tirad Concepcion, *Santos 5678* (US); Lepanto, Cervantes Trail, *Ramos & Edano 38103* (GH); Zambales, *Ramos 5044* (NY, US).

All collections of *Mussaenda lanata* are similar in their distinguishing characters, having large, membranous, densely pubescent leaves, acuminate stipules which are hairy and faintly bifid at the apex, crowded inflorescence with short campanulate flowers and small corolla lobes, and larger fruits bearing small seeds with 3 to 6 or 2 to 5 foveae in the areoles of the testa. The usual variations are in the size and shape of the leaf and in the fruit. The seeds are small and characterized by 3 to 6 foveae in the areoles of the testa. The collection, *Ramos 5044*, however, differs slightly in that its seeds are larger (0.64–0.67 mm. long, 0.5–0.56 mm. broad) and contain 2 to 5 foveae in the areoles of the testa.

Robinson (1911) stated that this species is allied to *Mussaenda anisophylla* and *M. villosa* Wall. It seems to me that its affinities are rather with *M. magallanensis* and to a lesser degree with *M. anisophylla* and not at all with *M. villosa*. The species agrees with *M. magallanensis* in the important characters of the stipule, calyx lobes, stamens, ovary, and seed. *Mussaenda villosa*, on the other hand, is a climber with broadly lanceolate bracts and bracteoles, recurved calyx lobes, and slender corolla tube, bearing smaller, glabrous berries with oblong, spiny seeds containing 2 to 8 foveae in the areoles of the testa. None of these characters are common to the two species.

9. **Mussaenda macrophylla** Wall. var. **brevipilosa**, var. nov. (TYPE: *Fenix 3770*).

*M. macrophylla* sensu Merr. Philip. Jour. Sci. Bot. **3**: 437. 1908 and Enum. Philip. Fl. Pl. **3**: 518. 1923, non Wall.

A typo differt stipulis et calycibus minoribus; pilis ad faucem corollae

longistylae brevibus, ad orifaceum non penicillatis; ovario obconico; fructibus lenticellatis; seminibus minoribus.

A large, subscandent shrub with stout branches densely pubescent with grayish hairs becoming rufous-brown when dry. Leaves ovate, elliptic, oblong, or elliptic-lanceolate, 10–26 cm. long, 5–15 cm. broad, glabrous on both surfaces but hairy on the veins beneath or pubescent on the upper surface and hirsute below, short-acuminate, cuneate at base, somewhat decurrent on the petiole, lateral veins 8–13 pairs, conspicuous beneath; petiole 0.6–4.2 cm. long, hairy. Stipules large, ovate or acuminate from a broad base, 7–12 mm. long, 3.5–7 mm. broad at the base, bifurcate to 1/4–2/3 their length from the apex, lobes straight, hairy on the outer surface, glabrous or pubescent within with numerous glands in 2 groups or in a continuous band. Inflorescence a terminal, spreading or somewhat compact, trichotomously branched, pubescent cyme; bracts and bracteoles lanceolate or ovate, acuminate, hairy, bracteoles deeply trilaciniate into lanceolate, acuminate lobes and broader at the base. Flowers large, heterostylous, nearly sessile or on very short, stout, pubescent pedicels shorter than the ovaries. Calyx lobes triangular-lanceolate or oblong-lanceolate, 3.2–8 mm. long, 1–2.5 mm. broad, acute or acuminate, hairy on both surfaces or on the outer surface only, glabrous within except at apex, with 1–5 pairs of glands at the base of each; petaloid sepal white, ovate, oblong or orbicular-ovate, 6.5–9 cm. long, 3.3–7 cm. broad, short-acuminate, acute or obtuse at apex, cuneate at base, glabrous on both surfaces except on veins beneath or puberulous on the upper surface and hirsute beneath, "petiole" 1–4 cm. long, hirsute. Corolla tube 2–3 cm. long, hairy on the outer surface, hairy within as far as the bases of anthers, hairs long in short-styled forms, short in long-styled forms and not tufted at the mouth of the tube; corolla lobes broadly ovate or orbicular, acute or apiculate, pubescent on the outer surface, papillate on the inner. Stamens with short filaments, epipetalous about 1/2 way or a little below the middle of the tube in long-styled forms, 3/5–2/3 of the way up in short-styled forms; anthers linear, dorsifixed, introrse, 5.5–6.7 mm. long, bilobed at the base. Ovary 4–5.5 mm. long, fusiform or obconical, hairy, 2-locular, with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.9 cm. and 0.7 cm. long respectively in long-styled forms, 3.8–8 mm. and 3–3.5 mm. long in short-styled forms. Berry ovoid or oblong-ovoid, 1.1–1.2 cm. long, lenticellate, sparsely hirsute with very broad nectariferous scars, calyx lobes deciduous; seeds minute, reticulate, 0.67–0.87 mm. long, with 2–6 foveae in the areoles of the testa.

DISTRIBUTION. This variety of *Mussaenda macrophylla* is confined to the islands of the Philippine group. It has been collected in flower from April to July and in fruit from August to October.

**Philippine Islands.** BATAN: *Fenix 3770* (NY–holotype, US–isotype), *Ramos 80071* (A). CALAYAN: *Velasco 26650* (US). CAMIGUIN: *Edano 79343* (A). LUZON: *Edano 79448* (A), *Ramos & Edano 29719* (A, US); Bohol, *Ramos*

*42577* (A). MINDANAO: *Ramos & Edano 85008* (A); Camiguin de Mindanao, *Ramos 14604* (US).

This variety differs in a number of characters from *Mussaenda macrophylla* var. *macrophylla* which is distributed from Nepal and Assam to Yunnan. It has smaller stipules, flowers, and calyx segments; the hairs inside the corolla tube in long-styled forms are short and not tufted at the mouth as compared to the long hairs which are tufted at the mouth in the typical form of var. *macrophylla*; the seeds are smaller, although the number of foveae in the areoles of the testa is the same in both varieties.

10. **Mussaenda magallanensis** Elmer, Leafl. Philip. Bot. 3: 996. 1911 (TYPE: *Elmer 12451*); Merrill, Enum. Philip. Fl. Pl. 3: 519. 1923. FIG. 1, d; FIG. 2, f, g, h.

*M. macrophylla* sensu Vidal, Phan. Cuming. Philip. 118. 1885, non Wall.

Shrub about 2–3 m. high with terete, densely pilose branches, hairs almost at right angles to the stem. Leaves oblong or elliptic, 6.5–28.5 cm. long, 3.5–13(–19.5) cm. broad, abruptly acuminate, base cuneate to obtuse, decurrent on petiole, hirsute on both surfaces with 10–13 pairs of lateral veins conspicuous beneath; petiole 0.6–3.5(–7.5) cm. long, stout, pilose. Stipules triangular-ovate, acuminate from a broad base, 7.5–16 mm. long, 4.5–9 mm. broad at the base, apex entire or bifid, densely hairy on the outer surface, pubescent within with numerous glands in a continuous band at the base. Inflorescence a terminal, hairy, di- or trichotomously branched corymbose cyme; bracts and bracteoles lanceolate, 5.5–11 mm. long, 1–2.2 mm. broad, hairy on both surfaces or on the outer surface only, bracteoles trilaciniate, lobes subulate. Flowers heterostylous on stout, pubescent pedicels shorter than the ovaries. Calyx lobes narrowly oblong-lanceolate or linear, 3.5–6 mm. long, 0.6–1.5 mm. broad, gradually tapering to a point, 3-striate towards the base, hairy on both surfaces with 1 or 2 pairs of glands at the base of each sepal. Petaloid sepal white, orbicular-oblong, elliptic or broadly ovate, acute, cuneate at base, glabrous, except on veins, on both surfaces, "petiole" 1.2–3.5 cm. long, hirsute. Corolla tube 2–3 cm. long, glabrous or with only straggling hairs on the outer surface, hairy within as far as the bases of the anthers or to about 1 mm. lower; hairs not tufted at the mouth, long in short-styled forms covering about 1/3 the tube from the top, short in long-styled forms extending to about 1/2 the length of the tube; corolla lobes orange, suborbicular-ovate, 3–3.5 mm. long, 2.7–4 mm. broad, rounded or apiculate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous 2/3 way up on the tube in short-styled forms and 1/2 way up in long-styled forms; anthers linear, dorsifixed, introrse, 3–4.5 mm. long, bifid at the base. Ovary turbinate, 3.2–4.5 mm. long, densely hairy, 2-locular with numerous ovules on axile placentae; style and stigma lobes 1.6 cm. and 6.5 mm. long respectively in long-styled forms, 1.5–6 mm. and 1.5–2.7 mm. long in short-styled forms. Berry ellipsoid, 1.2–2.2 cm. long, hairy when

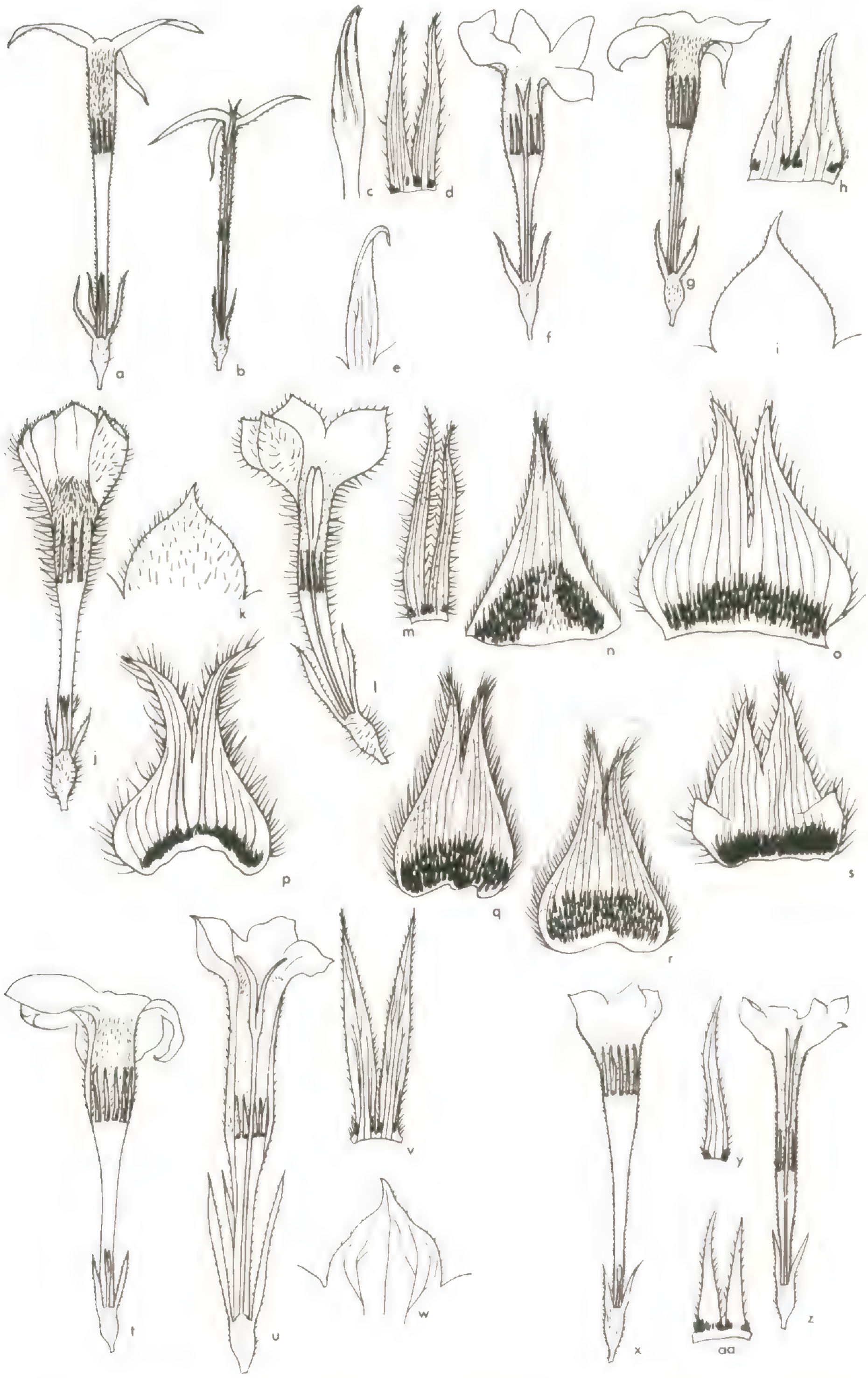


FIG. 3. Longitudinal sections of the long-styled and short-styled flowers of some Philippine species of *Mussaenda*, calyx and corolla lobes seen from within, and variations in the stipules of *M. anisophylla*. a–e, *M. albiflora*: a (*Ramos & Edano 31107*), × 1; b (*Dias 29885*), × 1; c (*idem*), apical portion of a flower

young, becoming sparsely pubescent, lenticellate, calyx lobes deciduous; seeds minute, reticulate, 0.5–0.67 mm. long, 0.33–0.53 mm. broad, oblong or oblong-ovate with 3–6 or 4–12 foveae in the areoles of the testa.

DISTRIBUTION. *Mussaenda magallanensis*, up to now considered as endemic to Mindoro and Sibuyan Islands, seems to extend to the neighboring islands of Luzon, Panay, and Leyte, growing along rivers, on mountain slopes, and in brushland from sea level up to an elevation of 300 meters. It has been collected in flower from January to May, in August, and from October to December; in fruit in January and from August to November.

**Philippine Islands.** LUZON: Laguna Prov., Mt. Banajao, *Ocampo 27899* (US), *Sulit 18877* (PNH, US); Isabela Prov., San Mariano, *Ramos & Edano 46977* (NY). MINDORO: Puerta Galera, *Britton 19422* (PNH), *Santos 5212* (US), *Ramos 46385* (NY); Baco River, *McGregor 131* (US, NY), *Merrill 4072* (US, NY), *1212* (US); Calapan, *Merrill 986* (GH, NY, US), *Merritt 6904* (US), *8779* (US); Bongabon and Pinamalayan, *Maliwanag 113* (PNH); Sablayan, Ligaya, *Reed 40896* (PNH), *40892* (PNH). SIBUYAN: Capiz Prov., Magallanes (Mt. Giting-giting), *Elmer 12451* (A–lectotype; GH, NY, US–isotypes). PANAY: Capiz Prov., *Edano 46114* (NY), *Escritor 21240* (US). LEYTE: *Wenzel 442* (A, US); Dagami, *Ramos 15328* (US).

*Mussaenda magallanensis* has affinities with *M. anisophylla* Vid. in the pubescence of the stem and leaves but differs from it in the entire or slightly bifid stipules, the 3-striate, linear or oblong-lanceolate sepals tapering to a point at the apex, and the glabrous or straggly-hairy corolla tube. Also it seems to be allied to *M. chlorantha* Merr. by the character of its stipules. *Wenzel 442* and *Ramos 15328* from Leyte differ from the type in the large leaves with longer petioles and seeds with testa bearing 3 to 6 foveae in the areoles. The specimen *Ramos & Edano 46977* differs slightly in its large leaves, the petaloid sepals, and the smaller calyx lobes.

This species is distinguished by the more or less horizontal pubescence on its stems and branches, the characteristic sepals and stipules, the large fruits with deciduous calyx segments, and the small seeds.

USES. The leaves of this species are used as a substitute for tobacco.

11. **Mussaenda milleri** Elmer, Leafl. Philip. Bot. 10: 3780. 1939.

Laxly branched undershrub about 3 m. high with few, widely spreading, subterete, gray to brown brittle branches, rebranching toward their ends.

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bud, × 2¾; d (*idem*), calyx lobes, × 3; e (*idem*), corolla lobe, × 1¾. f–i, *M. philippica*: f (*Elmer 7045*), × 1; g (*Ramos 17447*), × 1⅕; h (*idem*), calyx lobes, × 3½; i (*idem*), corolla lobe, × 4. j–s, *M. anisophylla*: j (*McGregor 23006*), × 1¼; k (*idem*), corolla lobe from back, × 2½; l (*Elmer 17481*), × 1; m (*idem*), calyx lobes, × 2½; n–s, stipules, n (*Merrill 2508*), × 2¾; o (*McGregor 23006*), × 3; p (*Elmer 17481*), × 2¾; q (*Borromeo 25602*), × 2¾; r (*Meyer 3020*), × 1¾; s (*Elmer 9154*), × 2½. t–w, *M. philippinensis*: t (*Sulit 18877*), × 1½; u (*Sulit & Conklin 17652*), × 1¾; v (*idem*), calyx lobes, × 2; w (*idem*), corolla lobe, × 5. x–aa, *M. benguetensis*: x (*Santos 5497*), × 1; y (*idem*), calyx lobe, × 3½; z (*Loher 1523*), × 1; aa (*idem*), calyx lobes, × 2½.

Leaves more or less clustered at the ends of branchlets, elliptic to ovate- or oblong-elliptic, 7–12 cm. long, 3–6 cm. broad, sharply acute or acuminately recurved at apex, cuneate at base, pubescent on both surfaces, densely so on veins beneath, midrib straight, sunken along the upper surface and filled with reddish-brown hairs; veins 5–11 pairs, ascending, curved, cross bars numerous, very evident on the lower surface; petiole 1–2 cm. long, reddish brown, hirsute. Stipules broadly lanceolate, 9–12 mm. long, 5–5.5 mm. broad, bifurcate 1/2 way or more, lobes lanceolate, covered densely on both surfaces with reddish-brown hairs, the base within somewhat glabrous with large, linear glands in 2 groups covered with finer hairs, base of the outer surface red streaked along with the hairs. Inflorescence terminal, corymbosely paniculate, hirsute, basal pair of branches subtended by foliaceous bracts, the upper branchlets with linear bracts similarly pubescent. Flowers on short, pubescent pedicels; calyx segments 3–5 mm. long, setaceously pointed; petaloid sepal occasional, yellowish white, subelliptic on a slender "petiole"; corolla slenderly tubular, 2–3 cm. long, hairy on the outer surface, lobes elliptic, orange-red, glabrous on the upper surface. Berry ellipsoid, narrowing towards the pedicel, 1.5 cm. long, lenticellate, reddish strigose-pubescent, calyx segments deciduous; seeds minute, reticulate, triangular-ovate, broader than long, 0.6–0.7 mm. long, 0.67–0.8 mm. broad, with 2–4(–6) foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Luzon, and grows upon the summit mountain ridge at about 1067 meters above sea level. It has been collected in flower in March and in fruit in August and September.

**Philippine Islands.** LUZON: Nueva Ecija Prov., Mt. Umingan, *Ramos & Edano 26468* (NY, US), Aug.–Sept. 1916, in fruit only.

The isotypes of *Mussaenda milleri* apparently were not distributed to herbaria in the U. S. A. and were unavailable for examination. *Ramos & Edano 26468* is nearest to the original description, agreeing with it in the form and pubescence of the leaves and stipules, but differing from it in the number of pairs of lateral veins in the leaf. As in the original description, the midrib is sunken on the upper surface and filled with reddish-brown pubescence. This collection was made much earlier than the type but not described, probably because of insufficient material. The holotype was destroyed in World War II; if isotypes are not located *Ramos & Edano 26468* (NY) should become the neotype.

*Mussaenda milleri* is similar to *M. nervosa* in its small leaves, midrib sunken on the upper surface, short corolla lobes, and fruits with deciduous calyx segments, but differs from that species in the characters of the stipules, calyx segments, and pubescence of the fruit. The species is distinguished from others by the smaller leaves with sunken midrib on the upper surface filled with reddish-brown pubescence, recurved leaf apices; characteristic broadly lanceolate stipules, hirsute with reddish-brown pubescence and streaked red on the outside; ellipsoid, lenticellate, strigose berries with deciduous calyx segments.

12. **Mussaenda multibracteata** Merr. Philip. Jour. Sci. Bot. 11: 34. 1916 (TYPE: *Ramos 23585*); Merrill, Enum. Philip. Fl. Pl. 3: 519. 1923. FIG. 4, f–n.

Shrub or small tree, 2–4 m. high with terete stems and densely hirsute branches, leaves, and inflorescences. Leaves membranous, ovate, oblong-ovate, or lance-elliptic, 9.5–30 cm. long, 4–16 cm. broad, acuminate at apex, cuneate at base or long attenuate and decurrent on petiole, prominently hirsute with spreading hairs on both surfaces especially along the veins, lateral veins 8–11 pairs, conspicuous beneath; petiole 1–9.5 cm. long, hirsute. Stipules ovate, 12.5–14 mm. long, 8–10 mm. broad at the base, acuminate, bifurcate from the apex for about 1/2–2/3 their length, hairy on the outer surface, usually glabrous within or hairy at the base only, with numerous glands in 2 groups. Inflorescence a terminal, di- or trichotomously branched, diffuse, densely hairy, cymose panicle; bracts and bracteoles subpersistent, numerous, crowded, lanceolate, 5–13 mm. long, acuminate, entire, bifid or trifid at apex, lateral lobes much shorter than the central one, hirsute on the outer surface, glabrous within with a tuft of hairs at the base. Flowers heterostylous, on stout, densely hirsute pedicels shorter than the ovaries. Calyx lobes broadly lanceolate, 6.7–28 mm. long, 1–6 mm. broad, acuminate, hirsute on the outer surface, sparingly pubescent or glabrous within with a tuft of hairs and 1 or 2 pairs of glands at the base of each; petaloid sepal ovate or elliptic, 5.5–10.5(–12.5) cm. long, 3–6(–9) cm. broad, acute or subacute at apex, cuneate at base, hirsute on both surfaces and 5-veined, "petiole" 2 cm. long, densely hirsute. Corolla yellow, the tube stout, 2.5–3.3 cm. long, densely hirsute on the outer surface with hairs almost horizontally spreading, hairy within 3/4 way down from the mouth of the tube in long-styled forms and 1/2 way in short-styled forms; hairs within not tufted at the mouth and shorter in long-styled forms; corolla lobes ovate or orbicular, 3.5–6 mm. long, 4.5–6 mm. broad, hairy on the outer surface, glabrous within. Stamens with short filaments, epipetalous below the middle of the tube 2/5–1/2 way up in long-styled forms and above the middle (2/3 way up) in short-styled forms; anthers linear, dorsifixed, introrse, 4.5–5 mm. long, bifid at the base. Ovary broadly or cylindrically turbinate, 4.5–6 mm. long, densely hirsute, 2-locular with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.7–2 cm. and 8.5–10 mm. long respectively in long-styled forms, 3 mm. and 2.5 mm. long in short-styled forms. Berry oblong or elliptic, 1.2–2 cm. long, hairy, lenticellate with persistent calyx segments; seeds minutely obnapiform, reticulate, 0.53–0.67 mm. long, 0.46–0.56 mm. broad, faintly spiny but not obvious, with 4–11 foveae in the areoles of the testa.

DISTRIBUTION. This species grows by streams or on damp slopes in the primary forests of Luzon and Catanduanes from 150 to 2100 meters elevation. It has been collected in flower from May to August, in fruit from July to September, November, and December.

**Philippine Islands.** LUZON: Albay, Mayon Volcano, *Mendoza 18431* (PNH,

US), *18376* (PNH); Tabayas, Mt. Binuang, *Ramos & Edano 28687* (A, US), *28783* (A, US); Mt. Tulaog, *Ramos & Edano 29093* (A, US); Casiguran, *Ramos & Edano 45480* (NY); Camarines Sur, Her-it River, *Edano 76425* (NY); Pili, Mambugna (Mt. Isarog), *Convocar 2820* (A, PNH); Cagayan, Mt. Dos Cuernos, *Ramos 77006* (PNH); Camarines Norte, Minasag River, *Edano 40230* (PNH); Isabela, *Clemens 17011* (NY); Sorsogon, *Ramos 23715* (US), *Ramos 23585* (NY–lectotype). CATANDUANES: *Ramos 30509* (A, US), *30262* (US); Mt. Tagmasuso, *Ramos & Edano 75259* (NY), *75159* (NY); Bato Trail to Viga, *Ramos & Edano 75143* (NY, US).

This species resembles *Mussaenda philippinensis* in its persistent, lanceolate sepals which are hairy on both surfaces. It differs considerably, however, in its characteristic pubescence, deeply bilobed stipules, longer corolla tube with lobes which are glabrous within, and the larger stamens, ovaries, fruits, and smaller seeds. *Mussaenda multibracteata* is characterized and distinguished from other species by its pubescence; large leaves; numerous, crowded, subpersistent bracts and bracteoles; large stipules which are glabrous within; broadly lanceolate, persistent sepals; hirsute petaloid sepals; corolla lobes glabrous within; large, hairy, lenticellate fruits and small, faintly spiny seeds with 4–11 foveae in the areoles of the testa.

13. **Mussaenda nervosa** Elmer, Leafl. Philip. Bot. 3: 994. 1911 (TYPE: *Elmer 10510*); Merrill, Enum. Philip. Fl. Pl. 3: 519. 1923.
FIG. 1, e; FIG. 2, i, j, k, ka.

Shrub 3 m. high with much-branched stems and erect branchlets. Leaves ovate-oblong or lance-elliptic, 6–15 cm. long, 2.5–5 cm. broad, acute or acuminate at apex, cuneate, acute or obtuse, and sometimes decurrent at the base, rugose and glabrous or pubescent on the upper surface, hairy on veins on the lower surface with 10–15 pairs of parallel curved-ascending lateral veins, very prominent beneath but sunken into the blade on the upper surface; petiole 0.5–4 cm. long, pubescent. Stipules deciduous, ovate-acuminate, 4–5.5 mm. long, 3.5 mm. broad at the base, bifurcate from the apex for about 1/2 their length, lobes slightly diverging, hirsute on the outer surface, glabrous within with a few glands in 2 groups at the base. Inflorescence an erect, terminal, dichotomously branched, pubescent cyme; bracts and bracteoles setose-acuminate, 0.7–1 mm. long, glabrous within. Flowers heterostylous, not clustered, on very short, stout, pubescent pedicels. Calyx lobes linear, laciniate, 11–16.5 mm. long, 0.7–1 mm. broad, with a prominent midvein terminating in a fine point, pubescent on the outer surface, glabrous or pubescent within, with or without a tuft of hairs, and with 1 or 2 pairs of glands at the base; petaloid sepal ovate, 5–8 cm. long, 3–5.2 cm. broad, glabrous on the upper surface, hirsute on veins beneath, cuneate at the base, "petiole" 1.2–3 cm. long, hirsute. Corolla tube 2.5–3 cm. long, subfalcate, hairy on the outer surface, hairy within as far as the bases of anthers or a little lower; hairs long in short-styled forms and short in long-styled forms, not tufted at the mouth. Corolla lobes

deep yellow, ovate-lanceolate or elliptic-acuminate, 8.5–9 mm. long, 4.5–5 mm. broad, hairy on the outer surface, granular within and 3- or 5-parallel-veined. Stamens with short filaments, epipetalous on the tube about 1/2 way up in short-styled forms, below the middle of the tube (about 2/5 way up from the base) in long-styled forms; anthers linear, dorsifixed, introrse, 6.5–7.5 mm. long, acute at apex and bifid at the base. Ovary broadly turbinate, 4–4.5 mm. long, hairy, 2-locular with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.7 cm. and 8.5 mm. long respectively in long-styled forms, 1.45 cm. and 2 mm. long in short-styled forms. Berry ellipsoid or globular, 1 cm. long, hairy when young, glabrous at maturity, lenticellate, calyx segments deciduous; seeds minute, reticulate, angularly globose, 0.46–0.6 mm. long, 0.36–0.43 mm. broad, with 4–12 foveae in the areoles of the testa.

DISTRIBUTION. This species grows on the islands of Luzon and Mindanao in forests up to an elevation of about 1200 meters above sea level. Elmer's type specimen was gathered from the densely forested basin of Mt. Apo in Todaya District. The species has been collected in flower in May, June, and July; in fruit in August and September.

**Philippine Islands.** LUZON: Nueva Ecija Prov., *Ramos & Edano 26422* (A, NY, US). MINDANAO: Bukidnon Subprov., *Ramos & Edano 39077* (A, US); Davao Dist., Todaya (Mt. Apo), *Elmer 10510* (A–lectotype; GH, NY, US–isotypes).

*Mussaenda nervosa* seems to be distantly allied to *M. philippinensis* with which it agrees only in the long calyx segments, and from which it differs considerably in the characters of the stipules, petals, and fruits. On the other hand it shows affinity to *M. milleri* in that both species are shrubs of comparable size, with the veins of the leaves sunken on the upper surface, which occur in the same locality in Luzon. *Mussaenda nervosa* differs from *M. milleri*, however, in the ovate-acuminate, short stipules, longer calyx segments, subfalcate corolla tube, smaller and glabrous fruits, and smaller seeds with a greater number of foveae in the areoles of the testa.

*Mussaenda nervosa* is distinguished from other species by the small leaves, with the midrib and 10 to 15 pairs of lateral veins sunken on the upper surface; small stipules glabrous within and with fewer glands; laciniate calyx segments; subfalcate corolla tube; glabrous and globular or ellipsoid berries with deciduous calyx segments, and small seeds with 4 to 12 foveae in the areoles of the testa.

14. **Mussaenda palawanensis** Merr. Philip. Jour. Sci. Bot. 10: 103. 1915 (TYPE: *Fenix 15531*); Merrill, Enum. Philip. Fl. Pl. 3: 519. 1923. FIG. 1, k.

Erect shrub 2–3 m. tall, more or less ciliate-hirsute in all parts with reddish-brown, terete, glabrous branches, the younger ones hirsute. Leaves oblong or oblong-ovate, 7–18 cm. long, 3–10 cm. wide, abruptly acuminate

at apex, rounded or cuneate at base, hairy on both surfaces, upper surface with scattered stiff hairs, lower surface with paler hairs also scattered, margins ciliate, lateral veins 9–14 pairs; petiole stout, 0.5–0.9 cm. long, hirsute. Stipules lanceolate, 8–10 mm. long, 4.5–8.5 mm. broad at the base, acuminate and bifurcate more than 1/2 their length from the apex,

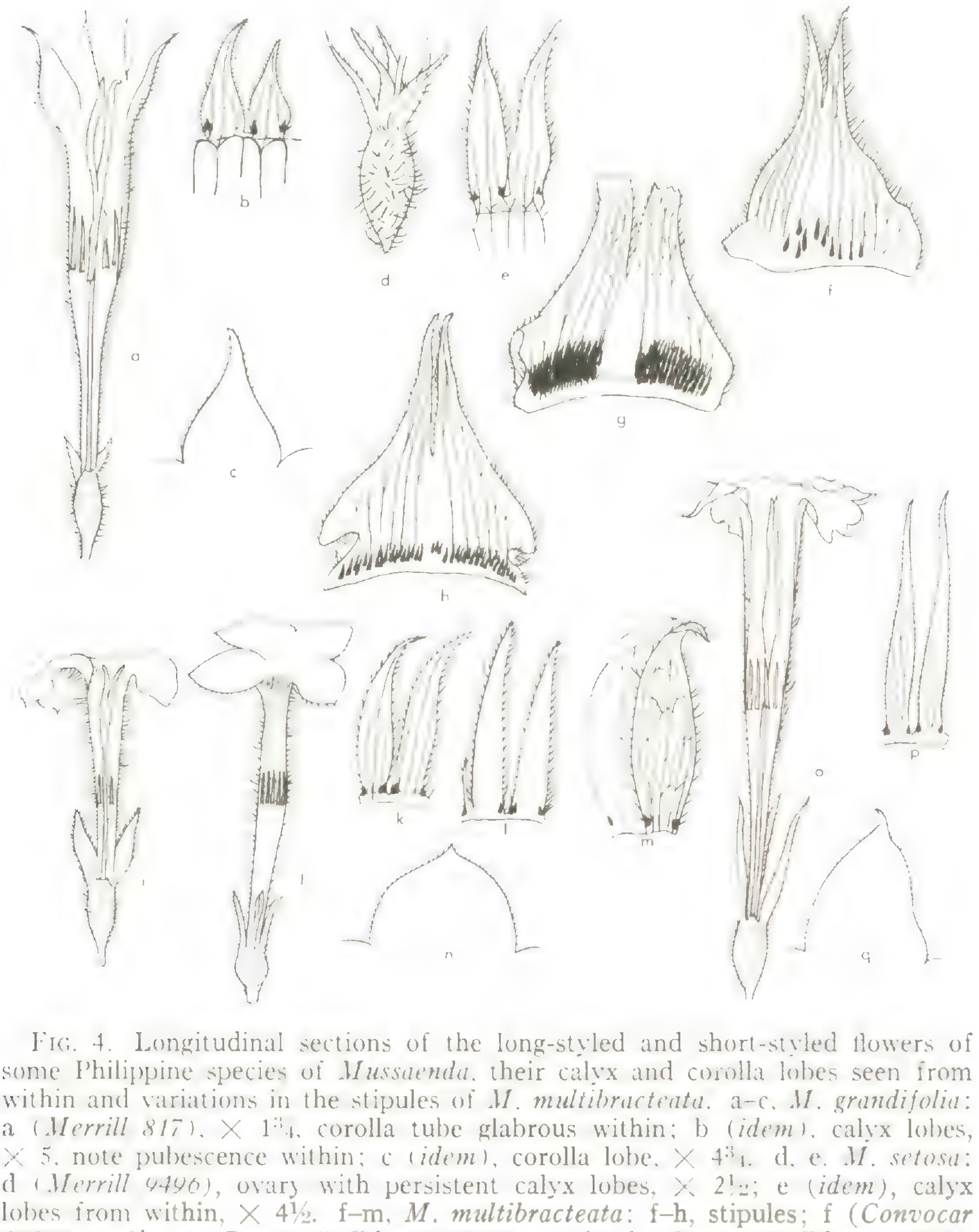



FIG. 4. Longitudinal sections of the long-styled and short-styled flowers of some Philippine species of *Mussaenda*, their calyx and corolla lobes seen from within and variations in the stipules of *M. multibracteata*. a–c, *M. grandifolia*: a (*Merrill 817*), × 1¾, corolla tube glabrous within; b (*idem*), calyx lobes, × 5, note pubescence within; c (*idem*), corolla lobe, × 4¾. d, e, *M. setosa*: d (*Merrill 9496*), ovary with persistent calyx lobes, × 2½; e (*idem*), calyx lobes from within, × 4½. f–m, *M. multibracteata*: f–h, stipules; f (*Convocar 2820*), × 2½; g (*Ramos & Edano 28783*), × 2½; h (*Ramos & Edano 29093*), × 2; i (*Convocar 2820*), × 1; j (*Ramos & Edano 28783*), × 1; k (*idem*), calyx lobes, × 2¾, glabrous within except for band of hairs at base; l (*Ramos & Edano 29093*), calyx lobes, × 2, hairy within; m (*Convocar 2820*), calyx lobes, × 2, note width and hairiness (hairs omitted from 1 lobe); n (*idem*), corolla lobe, × 3½. o–q, *M. acuminatissima*: o (*Ramos 33133*), × 2; p (*idem*), calyx lobes, × 2½; q (*idem*), corolla lobe, × 4½.

lobes subulate and diverging, hirsute on the outer surface, glabrous within except at the base among the few glands occurring in 2 groups. Inflorescence of terminal, few-flowered, densely hirsute cymes, flowers usually in crowded terminal clusters; bracts and bracteoles lanceolate, 3.5–6 mm. long, hairy on both surfaces, bracteoles trifid, lateral lobes very short. Flowers heterostylous on stout, pubescent pedicels shorter than the ovaries. Calyx lobes lanceolate, 6.7–10.5 mm. long, 2–2.5 mm. broad, slenderly acuminate, hairy on both surfaces, hairs shorter within and scantier, with 3 or 4 pairs of glands at the base of each; petaloid sepal white, broadly ovate, 6–12 cm. long, 4–9 cm. broad, bluntly acuminate at the apex, cuneate at the base, puberulous on the upper surface, hirsute beneath; "petiole" 1–1.5 cm. long, hirsute. Corolla white to bright orange, the tube 2–2.2 cm. long, infundibuliform, appressed hirsute on the outer surface, hairy within 1/2 way in long-styled forms and 1/3 way from the top in short-styled forms, hairs not tufted at the mouth and shorter in long-styled forms; corolla lobes ovate, 6 mm. long, 4 mm. broad, prominently acuminate or caudate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous on the tube just above the middle in long-styled forms and 2/3 way up in the broader portion in short-styled forms; anthers linear, dorsifixed, introrse, 5–6.5 mm. long, bifid at the base. Ovary cylindric-turbinate, 4.5–6 mm. long, densely hirsute, 2-locular with numerous ovules on axile placentae; style and stigma lobes 1.4 cm. and 6.5 mm. long respectively in long-styled forms, 3.5 mm. and 3.2 mm. long in short-styled forms. Berry ovoid or obovoid, 1.2–1.4 cm. long, pubescent, lenticellate, calyx segments deciduous; seeds minute, reticulate, broadly triangular-ovate, broader than long, 0.6–0.77 mm. long, 0.73–0.83 mm. broad; with 3–6(–8) foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to Palawan where it occurs in thickets and old clearings up to an elevation of about 150 meters above sea level. It has been collected in flower in February, July, August, and December; in fruit in December.

**Philippine Islands.** PALAWAN: San Antonio Bay, *Merrill 867* (US); Baraki, *Fox 13354* (A, PNH); Mt. Ibusi, *Ebalo & Conklin 1227* (A); Point Separacion, *Fenix 15531* (US–lectotype); Puerto Princesa, *Kondo & Edano 36685* (PNH); Mt. Kabangaan, *Edano 77718* (A); Brooke's Point, *Edano 244* (A, PNH).

Of the collections examined *Ebalo & Conklin 1227* differs from the lectotype in that its leaves are larger (18 cm. long), petaloid sepals 12 cm. long, stipules broader, and it bears orange flowers while it agrees in all other characters. The fruits of *Fox 13354* are larger (1.2–1.4 cm. long) than described for the type. *Kondo & Edano 36685* also possesses larger fruits but its leaves are obovate-lanceolate, resembling those of *Mussaenda attenuifolia*.

The species is closely allied to *Mussaenda philippica* from which it differs in the pubescence of the leaves, size and form of calyx and corolla segments, and in the seeds which, however, resemble those of *M. benguetensis*. It is distinguished from the other species by the characteristic

ciliation of its short-petioled leaves; lance-acuminate, bifurcate stipules with diverging, subulate lobes; broadly lanceolate sepals; short, thick, appressed-hirsute corolla tube; and scantily pubescent, ovoid berries with deciduous calyx segments.

15. **Mussaenda philippica** A. Rich. Mém. Soc. Hist. Nat. Paris **5**: 245. 1834 (TYPE: *Perrottet*); Merrill, Enum. Philip. Fl. Pl. **3**: 519. 1923. FIG. 1, j; FIG. 3, f, g, h, i.

*M. acutiflora* Bartling ex DC. Prodr. **4**: 370. 1830.
*Calycophyllum grandiflorum* Meyen, Reise **2**: 234. 1835.
*M. frondosa* sensu Blanco, Fl. Filip. 167. 1837; ed. 2. 118. 1845; ed. 3. **1**: 211. *pl. 58*. 1877, non L.
*M. glabra* sensu Fernandez-Villar, Novis. App. 108. 1880, non Vahl.
*M. grandiflora* Rolfe, Jour. Linn. Soc. Bot. **21**: 311. 1884.

Shrub or small tree 2–8 m. tall with terete or subterete, more or less pubescent or nearly glabrous, brown or gray, ascending, lenticellate branches. Leaves very variable, ovate, oblong-ovate or -lanceolate or obovate-oblanceolate, strongly conduplicate on the upper side, 3.5–23.5 cm. long, 1.7–12 cm. broad, acuminate at apex, cuneate or long attenuate at base, glabrous or scantily pubescent on the upper surface, glabrate on the lower surface, minutely pubescent or hirsute especially along the veins, lateral nerves 6–15 pairs, arcuate; petioles 0.3–2.5(–7.5) cm. long, minutely appressed pubescent or hirsute. Stipules oblong-ovate or acuminate from a broad base, 3–10.5(–12.5) mm. long, 2.2–7 mm. broad at the base, bifurcate from apex 1/4–3/4 their length, lobes not diverging and somewhat straight, pubescent on the outer surface, glabrous within, hairy throughout or at the base only and among the glands occurring in 2 groups. Inflorescence a terminal, di- or trichotomously branched, many- or few-flowered cyme; bracts and bracteoles lanceolate or ovate, 3–5 mm. long, hairy on the outer surface, glabrous within. Flowers heterostylous on stout, pubescent pedicels shorter or longer than the ovaries. Calyx lobes triangular or lance-acuminate, 1.2–7.5 mm. long, 0.5–1.5 mm. broad, hairy on the outer surface, glabrous or pubescent within with 2–5 pairs of glands at the base of each; petaloid sepal ovate or orbicular-ovate, 4–13 cm. long, 3–8.5 cm. broad, acute or subacute at apex, abruptly cuneate at base, glabrous on both surfaces or puberulous on the upper surface and hairy beneath, "petiole" 1–2 cm. long, pubescent. Corolla tube pale green, 2–3.5 cm. long, minutely appressed pubescent or hirsute on the outer surface, hairy within as far as the bases of the anthers, hairs within longer in short-styled forms than in long-styled forms, not tufted at the mouth; corolla lobes orange, lanceolate, ovate, or orbicular, 2.5–8(–12) mm. long, 2–5.5 mm. broad, apiculate, acuminate or somewhat caudate, hairy outside, papillate within. Stamens with short filaments epipetalous on the corolla tube 1/2–3/4 way up in short-styled forms and at about the middle in long-styled forms; anthers narrowly linear or lance-linear, dorsifixed, introrse, 6–8.5 mm. long in short-styled forms, 4–6 mm. long in long-

styled forms, acute or blunt at apex, bilobed at the base. Ovary broadly fusiform, oblong-turbinate or oblong, 3.5–7.5 mm. long, minutely appressed pubescent or hirsute; style and stigma lobes 1.5–2.9 cm. and 3–7.5 mm. long respectively in long-styled forms, 2.5–8.5 mm. and 2–4.5 mm. long in short-styled forms. Berry globular, 1–1.6 cm. long, glabrous or scantily pubescent, lenticellate, calyx segments deciduous; seeds minute, reticulate, not spiny, 0.6–1.0 mm. long, 0.39–0.8 mm. broad, testa with 2–5(–7) foveae in the areoles.

ILLUSTRATIONS. Blanco, Fl. Filip. ed. 3. 1: *pl. 58.* 1877; Vidal, Synopsis de familias. Atlas *pl. 56, f.* 1883 (not seen); Sulit, Philip. Jour. Forestry 2(1): 43. *pl. 3, fig. 2.* 1939.

DISTRIBUTION. This species has a very wide distribution. It occurs in almost all the islands of the Philippines, extending from Luzon to Palawan and Mindanao, eastward to Palau and Yap islands of the Caroline Group, and southward in the Solomon and Fiji islands, from sea level to an altitude of about 700 meters. It is a common shrub found along forested ridges, slopes and streams in old second-growth jungles and also in rugged, open, rolling country. It has been collected in flower and fruit throughout the year.

**Philippine Islands.** BATAN: Mt. Iraya, *Ramos 80283* (A). LUZON: Cagayan Prov., Littoc, *Adduru 142* (A, US); Lagum, *Adduru 218* (A, US); *Velasco 24852* (NY); Rizal Prov., Antipolo, *Vidal 389c* (A), *Ramos & Edano 29536* (A, US), *45292* (NY), *Reillo 19245* (US); west of Famy, *Brenner, Jr. 2584* (PNH), *Ramos 34* (US), *13573* (US); San Mateo, *Ahern's Collector 119* (US); Bosoboso, *Merrill 2655* (NY, US), *Vidal 1457d* (A); Camarines Prov., Nueva Caceres, *Vidal 1457bis* (A); Dalupaon-Paracao, *Ahern 818* (US), *802* (US); Dact, *Hallier* (NY); Kamugong River, *Edano 75879* (NY); Paracale, *Ramos & Edano 33520* (US), *33469* (NY); Carambola, Pili, *Convocar 2945* (A, PNH); Mt. Isarog, *Merrill, Species Blancoanae 413* (A, GH, NY, US); Sorsogon Prov., *Curran 10535* (NY, US); Irosin, *Edano & Gutierrez 37744* (PNH), *38555* (A, PNH); Mt. Bulusan, *Elmer 14388* (A, C, GH, NY, US); Tabayas Prov., *Manuel 23486* (US); Guinayangan, *Vidal 801* (A); Baler, *Escritor 21192* (US); Lucena, *Merrill 2890* (NY, US); Sariaya, *Whitford 559* (US); Bulacan Prov., Quingua, *Vidal 1457c* (A); Angat, *Vidal 389e* (A); Malinto, *Robinson & Merritt 6128* (GH); Laguna Prov., Los Banos, *Elmer 8134* (NY), *Steiner 40063* (PNH), *Holman 43* (GH); Mt. Makiling, *Elmer 17670* (A, GH, NY, US), *Sulit 9747* (A, PNH), *Mendoza 12224* (US); Makiling National Park, *Salvoza 3214* (PNH); Pangil, *Ramos 39882* (PNH); Bataan Prov., *Pascual 28682* (A), *23071* (A); Mt. Mariveles, *Elmer 6673* (NY); Lamao River, *Williams 127* (NY, US), *Whitford 388* (NY, US), *524* (NY, US), *Borden 1220* (NY, US), *Bartlett 14653* (A); Bagac, *Udasco 27292* (A); Albay Prov., Mayon Volcano, *Mendoza 18350* (PNH); Isabela Prov., Palanan, *McGregor 10726* (NY); Apayao Subprov., *Fenix 28234* (A, US); Cavite Prov., *Ramos & Deroy 22518* (US); Manila, San Francisco, *Loher 1520* (US); Novaliches, *Loher 1519* (US). ALABAT: *Ramos & Edano 48089* (NY). CATANDUANES: *Ramos 30452* (US). MARINDUQUE: *Vidal 1457* (A). MINDORO: Mansalay, *Merrill 912* (GH, NY, US); Mt. Yagaw, *Sulit & Conklin 16840* (A), *16875* (PNH); Sablayan, Ligaya, *Reed 40895* (PNH); Bulalacao, Padam Mt., *Ebalo 254* (A). SAMAR: *Vidal 389bis* (A), *Ramos 17447* (US); Catubig River,

*Edano 24806* (US), *Sablaya 45* (A), *Ramos 24174* (A, US); Tubabau Island, *Quisumbing 2045* (A); Matuguinao, Baruz, *Gachalian 1548.3* (PNH); Oras, Cadapnan, *Castro & Anonuevo 5782* (A); Catarman, Mt. Cansayao, *Sulit 14449* (PNH), *Alcasid & Oano 39863* (PNH); Laquilacon, *McGregor 43797* (NY), *Sulit 6125* (A, PNH); Borongan, Tagaslian, *Castro & Anonuevo 5810* (A), Pinamgasan, *Castro & Anonuevo 5853* (PNH). BILIRAN: *McGregor 18813* (A, US). BUSUANGA: *Ramos 41262* (A), *41236* (A, US). CULION: *Bermejos 182* (GH, NY, PNH, US). PANAY: Capiz Prov., *Edano 46220* (NY); Dumarao, *Talcon 22279* (PNH), *33828* (PNH); Libacao, *Martelino & Edano 35331* (NY); Antique Prov., *McGregor 32540* (US). GUIMARAS: *Gammill 261* (NY, US). LEYTE: *Wenzel 57* (A, GH, US), *179* (A, GH, US); Palo, *Elmer 7045* (A, NY). NEGROS: Mt. Katugasan, *Edano 21809* (PNH), *21782* (PNH); Dumaguete (Cuernos Mts.), *Elmer 10121* (A, NY, US). PALAWAN: *Foxworthy 605* (GH, NY, PNH, US), *691* (NY, US), *Bermejos 350* (GH, NY, US), *Curran 4517* (NY, US); Taytay, *Merrill 9332* (A, GH, NY, US); Puerto Princesa, *Cenabre 29149* (A); *Danao 19907* (NY, US); Mt. Pulgar, *Elmer 12792* (A, GH, NY, US). MINDANAO: *Decora & Hoover 172* (US), *163* (US); Agusan Prov., Cabadbaran (Mt. Urdaneta), *Elmer 13301* (A, GH, NY, US); Davao Prov., Madam, *Edano 1312* (A, PNH); Catalnan, *Kanehira 2497* (NY); Magdug River, *Edano 11074* (A); Santa Cruz, *Williams 2854* (NY, US); Cotabato-Dansalan, *Zwickey 34* (A, NY); Davao Dist., *Copeland 355* (NY, US); Surigao Prov., *Ahern 339* (US); Mt. Cantugas, *Ramos & Convocar 83500* (A); Butuan Subprov., *Miranda 20580* (US); Misamis Prov., Mt. Malindang, *Mearns & Hutchinson 4716* (NY, US); Zamboanga Prov., Margosa Tubig, *Guerrero 29549* (A); Dikus, *Frake 38115* (A, PNH), *Frake 36058* (PNH). BALABAC: *Vidal 389d* (A); *Mangubat 481* (US). CAGAYAN: Sulu, *Mearns 36* (US), *37* (US), *Warburg 14896* (A). PALMAS: *Merrill 5338* (NY, US).

**Caroline Islands.** YAP: Mt. Matade, *Fosberg 25555* (NY); Balabat, *Takamatsu 1872* (A). PALAU: *Fosberg 25769* (NY); *Takamatsu 1151* (A).

**Solomon Islands.** BOUGAINVILLE: Kupei Gold Field, *Kajewski 1666* (A). SANTA YSABEL: Meringe, *Brass 3538* (A). OWA RIKI: *Brass 3075* (A).

**Fiji Islands.** WAYA: *Fosberg 18008* (A).

From an examination of over 200 collections of this species from the different islands of the Philippines, the Caroline Group, Fiji, and the Solomon Islands it is evident that some are allied to *Mussaenda glabra*, others to *M. palawanensis*, and still others rather distantly to *M. macrophylla*, *M. philippinensis*, *M. pinatubensis*, and *M. anisophylla*.

The collections *Elmer 12792*, from Palawan; *Brass 3538* and *3078*, from the Solomon Islands; *Merrill 912*, from Mindoro; *Elmer 14388*, *Curran 10535*, *Fenix 28234*, *Merrill 413*, *Convocar 2945*, etc., from Luzon; and *Fosberg 25555*, *25769*, *Takamatsu 1151*, *1872*, from the Caroline Islands, bear resemblance to *Mussaenda glabra* in that their leaves are glabrate, minutely appressed pubescent on veins beneath, their stipules small and lanceolate with few glands at the bases within, and the corolla tubes are also minutely pubescent with short, lanceolate lobes. They differ, however, in the size and the venation of the leaves, the length of the corolla tubes, petals, anthers, etc.

The collections *Addurn 142*, *Elmer 17670*, *Whitford 524*, *Ramos 29882*, *Robinson & Merritt 6128*, etc., are allied to *Mussaenda palawanensis*. Their leaves are pubescent on both surfaces, densely so on the lower sur-

face, the sepals are broadly lanceolate, acuminate, hairy on both surfaces, and the petals are ovate and prominently acuminate. They differ in their longer petioles, shorter calyx lobes, and less hirsute corolla tubes.

One collection, *Merrill 5338*, from Palmas Islands, bears sepals similar to those of *Mussaenda philippinensis* but differs in numerous other characters which establish that it is *M. philippica*. *Edano 46220* and *Warburg 14896* have some resemblance to *M. macrophylla* in the pubescence of their stems and inflorescences, and in their orbicular-apiculate petals. *Merrill 2655*, from Luzon, bears affinities to *M. pinatubensis* in that its branchlets are erect, opposite, and terminated by leaves and the flower-bearing portion. It has small leaves, and the older pairs of stipules are fused around their nodes. The specimen *Edano & Gutierrez 37744* has spreading hairs on the stem and deeply bifurcate stipules hairy on both sides, characters of *M. anisophylla*.

The collections *Brass 3075* and *3538*, from the Solomon Islands, which resemble *Mussaenda glabra* in external characters, are related by other characters to *M. frondosa* L. in that the throat hairs of the corolla tube are long in the long-styled forms and extend below the bases of the anthers.

Throughout the species the seed character seems to be constant, though the seeds themselves vary in size and shape. The testa is foveolate with 3–5(–7) foveae in the areoles. *Cortez & Fernandez 34388* bears smaller fruits (0.8 cm. long) and somewhat spiny seeds with 3 to 10 foveae in the areoles of the testa, while *Frake 36058* also bears smaller fruits but has larger seeds (0.73–0.93 mm. long) with rugose testa.

From the foregoing it is evident that at least two genetic lines are involved in the evolution of this species: *M. glabra* coming down from the mainland of China and *M. palawanensis* from Palawan.

*Mussaenda philippica* is distinguished from other species by its ascending, freely rebranching branchlets; its glabrous or pubescent leaves recurved and strongly conduplicate; its erect green inflorescences and corolla tubes; its large anthers; its glabrous, lenticellate fruits with deciduous calyx segments; and its small, smooth seeds with reticulate testa bearing 2–5(–7) foveae in the areoles.

USES. The plant is used medicinally for stomach-ache in the Fiji Islands. The juice of the bark is used as a cure for headache in Mindoro. The leaf is employed as a substitute for tobacco, while in Mindanao the whole plant is used in agricultural rituals.

**Mussaenda philippica** forma **aurorae** (Sulit), stat. nov.

*M. philippica* A. Rich. var. *aurorae* Sulit, Philip. Jour. Forestry **2**(1): 39. *pl. 3, fig. 1.* 1939 (TYPE: *Mabesa 24876*).

Shrub 1–3 m. high with terete, pubescent branches. Leaves ovate or elliptic, 8–16 cm. long, 3.2–8.5 cm. broad, abruptly acuminate, cuneate at base, glabrate on the upper surface, pubescent beneath with 8–10 pairs of lateral veins; petiole 0.7–1.5 cm. long, hirsute. Stipules ovate, 7–9 mm. long, 5–6 mm. broad at the base, hairy on the outer surface, glabrous

within except below the glands, acuminate, bifurcate from apex 1/3–1/2 their length. Inflorescence a terminal, pubescent, few-flowered cyme; bracts and bracteoles lanceolate, 3.5–4 mm. long, hairy. Calyx lobes when unexpanded linear or lanceolate, 3–6 mm. long, 1 mm. broad; when expanded white, oblong, "petioled," 3.5–9 cm. long, ± 1.5–5.5 cm. broad, pubescent on both surfaces, 5-veined, stipe ± 1 cm. long, hairy. Corolla tube 2.5–3 cm. long, broader at the top, hairy on the outer surface, hairy within as far as the bases of the anthers; corolla lobes yellow, ovate, 4.5–6 mm. long, 4–5 mm. broad, apiculate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous 2/3–3/5 way up on the corolla tube; anthers linear, dorsifixed, introrse, 7–8 mm. long, blunt at apex, bilobed at the base. Ovary turbinate, 3.5 mm. long, hairy, 2-locular and with axile placentation; style and stigma lobes each 3.5 mm. long, the latter appressed on their receptive surfaces.

DISTRIBUTION. *Mussaenda philippica* forma *aurorae* was first collected by Mabesa at the foot of Mt. Balong-bulo, Laguna Province, in 1915. It was collected in 1930 by Curran in Sitio Buot, Makiling National Park, growing at an elevation of 100 meters above sea level. Now it is much cultivated as an ornamental shrub. It has never set seed and all plants in cultivation have been raised vegetatively from Curran's plant which was transplanted into the Forestry Nursery and propagated.

**Philippine Islands.** LUZON: Laguna Prov., *Mabesa 24876* (A–lectotype; US–isotype); Los Banos, Forestry College, *Walker 7456* (US), *Steiner 1743* (PNH); Manila Garden, *Quisumbing 2101* (PNH), *Steiner 2950* (A); Malacanan Grounds, *Quisumbing 4334* (A).

Forma *aurorae* differs from *Mussaenda philippica* forma *philippica* in the one to five expanded calyx segments in the flowers of an inflorescence but resembles it in all other characters. It is a short-styled form and has never produced fruit. Though the ovary contains ovules, the stigma lobes seem to remain appressed on their receptive surfaces, preventing pollination. Cuttings of this plant sent by Dr. L. H. McDaniels to the Fairchild Tropical Garden, Florida, from the Philippine Islands in 1959, were successfully rooted and multiplied. As a male parent it has been used to good effect in the Philippine Islands in crosses with *M. erythrophylla* Schum. & Thonn., an African species with the petaloid sepal crimson, producing a number of cultivars. The two most outstanding of these are called *Mussaenda* 'Luz' or 'Dona Luz' and *Mussaenda* 'Alicia' or 'Dona Alicia,' both of which are much cultivated for their ornamental qualities. In the former all five calyx segments are deep rose-purple and petaloid while in the latter only one segment is petaloid.

16. **Mussaenda philippinensis** Merr. Philip. Jour. Sci. Bot. 3: 264. 1908 (TYPE: *Merrill 4139*); Merrill, Enum. Philip. Fl. Pl. 3: 520. 1923. FIG. 1, n, o, p; FIG. 3, t, u, v, w.

Shrub 1–4 m. high with more or less hirsute, terete branches. Leaves

membranous, oblong-elliptic, 9.5–20 cm. long, 3.8–10 cm. broad, nearly glabrous or scantily pubescent on the upper surface, hirsute on veins of the lower surface with scattered hairs on the lamina, acuminate at apex, cuneate at base or long decurrent on the petiole, veins 8–12 pairs, petiole 0.3–4 cm. long, hairy. Stipules lance-ovate, acuminate, 9–13 mm. long, 4.5 mm. broad at the base, hairy on both surfaces, entire or faintly bifid at the tip with numerous glands in a continuous band at the base, ascending in the middle. Inflorescence a terminal, hirsute, dichotomously branched, somewhat compact, cymose panicle; bracts and bracteoles deciduous, linear-lanceolate, hirsute; bracteoles trilaciniate, lobes narrow, acuminate. Flowers heterostylous on stout, pubescent pedicels shorter than the ovaries. Calyx lobes narrowly lanceolate, 10.5–15 mm. long, 1 mm. wide, hairy on the outer surface, glabrous within or pubescent with 2 or 3 pairs of glands at the base of each sepal; petaloid sepal white, ovate or elliptic, 5–9 cm. long, 3–6 cm. broad, acute or subacute at apex, cuneate at the base, glabrous on the upper surface, hirsute on veins beneath, "petiole" 1.7–2.5 cm. long, hirsute. Corolla tube yellow, 2–2.5 cm. long, pubescent on the outer surface with short appressed hairs mixed with few long spreading ones, hairy within as far as the bases of the anthers, not tufted at the mouth; hairs shorter in long-styled forms than in short-styled forms, glabrous below the anthers; corolla lobes ovate, 1.5–3 mm. long, 2.2–3 mm. broad, acute or acuminate, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous on the tube below the middle, 2/5 way up in long-styled forms and 3/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 3–5 mm. long, abruptly acute at apex, bifid at base. Ovary obconical or turbinate, 3–3.5 mm. long, scantily appressed hairy, 2-locular with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.9 cm. and 6.5 mm. long respectively in long-styled forms, 1–2 mm. and 1.5–2 mm. in short-styled forms. Berry elliptic, 1.3–1.5 cm. long, rugose, scantily pubescent with persistent calyx segments; seeds minute, reticulate, broadly oblong or angularly globose, 0.6–0.67 mm. long, 0.46–0.6 mm. broad, with 3–8 foveae in the areoles of the testa.

DISTRIBUTION. This species grows in partial shade along creeks and ridges of second-growth forests from 10 to 300 meters elevation above sea level. It is confined to the islands of Luzon, Alabat, Mindoro, Semirara, and Panay. It has been collected in flower from April to July; in fruit in June, November, and December. The original description is based on a single collection from Semirara.

**Philippine Islands.** LUZON: Apayao Subprov., Mt. Duraragan, *Edano 19875* (PNH), alt. 300 m. ALABAT: *Merrill 10437* (A, NY, PNH, US). MINDORO: Mt. Yagaw (eastern slope), *Sulit & Conklin 17652* (A, PNH), alt. 267 m., *16875* (A), alt. 300 m.; Oyon Creek, *Paniza 9436* (A, PNH), alt. 10 m., *Ebalo 193* (A, PNH). SEMIRARA: *Merrill 4139* (NY–lectotype). PANAY: *McGregor 32449* (A, US).

Several collections have been erroneously placed in this species which should be referred to *Mussaenda magallanensis*. The collection *Merrill*

*10437* (A, NY, PNH, US) from Alabat Island possesses large, lance-elliptic leaves with the characteristic pubescence and hairy, lenticellate berries with persistent calyx segments, apparently resembling this species, but an examination of the seed indicates that it is nearer *M. magallanensis*. Its seeds are black, smaller (0.46–0.6 mm. long), obtusely 3- or 4-sided, testa faintly spiny with 4–12 foveae in the areoles. *McGregor 32449* (A, US) from Panay seems to be a variation from the type collection, differing from it in the shorter calyx segments (8 mm. long) and larger, acuminate petals (6 mm. long).

*Mussaenda philippinensis* seems to be allied to *M. magallanensis*, on the one hand, and to *M. wrayii* King, from the Malay Peninsula, on the other. It is distinguished by its entire or almost entire stipules, compact inflorescence, long, persistent calyx lobes, large fruits with small seeds, and 3–8 foveae in the areoles of the testa.

17. **Mussaenda pinatubensis** Elmer, Leafl. Philip. Bot. 9: 3210. 1934 (TYPE: *Elmer 21978*).

Shrub with spreading main branches dividing to terminate in glabrous, subangular, erect, short branchlets. Leaves opposite, often unequal, 4–8.3 cm. long, 2–3.7 cm. broad, slenderly or sharply acuminate at the apex but obtuse in many of the smaller leaves, cuneate at base, glabrous or puberulous on the upper surface, short-hairy on veins and venules beneath, lateral veins 6–11 pairs, ascending; petiole 3–10 mm. long, grooved above, sparsely strigose beneath. Stipules lanceolate, 5–8.5 mm. long, 2.5 -5 mm. broad at the base, bifid from the apex for about 1/5 their length, teeth terminating in a gland, hairy on the outer surface, hairy within at the base and apex, glands many in 2 groups, opposite pairs of older stipules fusing at their edges at the base to form a ring around each node. Inflorescence a terminal, dichotomously branched, many-flowered, minutely appressed-pubescent cyme almost equalling the leaves in length; bracts and bracteoles lanceolate or linear, 5–6 mm. long, hairy. Flowers probably heterostylous on stout, appressed-pubescent pedicels about 3 mm. long. Calyx lobes persistent, linear subulate, 7.7–8 mm. long, 1 mm. broad at the base, hairy on the outer surface, glabrous within; petaloid sepal yellowish-white, ovate or broadly lanceolate-elliptic, 5–8 cm. long, 2.5–3.6 cm. broad, acuminate, cuneate at base, glabrous on both surfaces, pubescent on the veins beneath; "petiole" 0.5–1.3 cm. long, hairy. Corolla deep yellow or orange, the tube 2–3 cm. long, appressed pubescent outside except at the subglabrous base, inside hairy as far as the bases of stamens, hairs long in short-styled forms (long-styled forms not seen), not tufted at the mouth; corolla lobes ovate, 4.5 mm. long, 4.2 mm. broad, apex acuminate-subcuspidate, strigose-hairy outside, papillate within. Stamens with short filaments, epipetalous 2/3 way up on the tube in short-styled forms; anthers linear, sub-basifixed, introrse, 5.5–10 mm. long, blunt at the apex and bifid at the sterile base. Ovary oblong, 4 mm. long, appressed pubescent, 2-locular with numerous

ovules on axile placentae; style 4 mm. long and stigma lobes 2.5 mm. long in short-styled forms. Berry not seen.

DISTRIBUTION. This species is endemic to Luzon where it grows on hot and dry river embankments at an elevation of about 1065 meters above sea level. It has been collected in flower in May.

**Philippine Islands.** LUZON: Pampanga Prov., Zambales Mountains (Mt. Pinatubo), *Elmer 21978* (PNH–holotype; A, GH, NY–isotypes).

At first no trace of Elmer's original collection was found, but a closer examination of the material available revealed that it had been placed under an unpublished name. Happily, the holotype of *Mussaenda pinatubensis* is still in existence, apparently having been on loan during World War II. It is allied to *M. nervosa* by its leaf and stipule characters and also to *M. philippica* but differs from the latter in the smaller leaves, longer calyx segments, and faintly bifid stipules. The species is distinguished from others in the small, glabrous or subglabrous leaves; lanceolate stipules faintly bifid at apex, each pair fusing at the base to form a ring around the node; linear-subulate, persistent calyx segments; ovate, subcuspidate corolla lobes; and oblong, scantily appressed-pubescent ovaries.

18. **Mussaenda scandens** Elmer, Leafl. Philip. Bot. **3**: 992. 1911 (TYPE: *Elmer 11291*); Merrill, Enum. Philip. Fl. Pl. **3**: 518. 1923. FIG. 1, g; FIG. 2, l, m, n, o, p.

*M. villosa* sensu Merrill, Philip. Jour. Sci. Bot. **5**: 243. 1910 and Elmer, Leafl. Philip. Bot. **3**: 992. 1911, non Wall.

Climber with numerous, curved, interlaced, lenticellate branches. Leaves ovate-elliptic or broadly oblong, 6–13.3 cm. long, 3–8 cm. broad, abruptly acute at apex, cuneate at base, obtuse or subrotund, pubescent on the upper surface, hairs short with few longer scattered ones, finely pubescent on the veins beneath with 6–10 pairs of lateral veins; petiole 0.3–1.5 cm. long, subglabrous or pubescent. Stipules deciduous, ovate-acuminate, 7–8 mm. long, 5 mm. broad at the base, bifurcate from apex more than 1/2 their length, lobes subulate, diverging, hairy on both surfaces, hairs within shorter with few glands in 2 groups at the base. Inflorescence a terminal, di- or trichotomously branched, appressed-pubescent, many-flowered, corymbose cyme; bracts and bracteoles lanceolate, acuminate, hairy on both surfaces, bracteoles broader, longer, and trilobed at apex. Flowers heterostylous, on stout, finely pubescent pedicels shorter than the ovaries. Calyx lobes linear-oblong, recurved, 3.5–5.5 mm. long, 0.8–1 mm. broad, sharply acuminate, hairy on both surfaces with 1 or 2 pairs of glands at the base of each sepal within; petaloid sepal ovate-elliptic, 6–7 cm. long, 3.8–4.5 cm. broad, puberulous on both surfaces, hairy on veins beneath, "petiole" 1–1.5 cm. long, pubescent. Corolla tube slender, 2–2.5 cm. long, hairy on the outer surface, hairy within 4/5 way down, glabrous at base;

hairs long in short-styled forms and short in long-styled forms, not tufted at the mouth; corolla lobes yellow, ovate, 2.5 mm. long, 2–2.5 mm. broad, acute, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous on the tube about 1/2 way in long-styled forms and a little higher in short-styled forms, adherent filaments free as loops on the tube for about 2 mm. midway between the base and the stamens; anthers linear, dorsifixed, introrse, 3.5–4.5 mm. long, bilobed at the base. Ovary turbinate, 3–3.5 mm. long, finely appressed pubescent, 2-locular with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.3 cm. and 6 mm. long respectively in long-styled forms, 4 mm. and 2.5 mm. long in short-styled forms. Berry ellipsoid, 1–1.3 cm. long, glabrous, calyx lobes deciduous; seeds minute, reticulate, ovoid, 0.83–0.9 mm. long, 0.67–0.7 mm. broad, spiny, with 3–9 foveae in the areoles of the testa.

DISTRIBUTION. This species is endemic to the island of Mindanao and grows in forests along streams at an altitude of 600 to 800 meters. It has been collected in flower in May, July, and August; in fruit in August, October, and November.

**Philippine Islands.** MINDANAO: Davao Dist., Todaya (Mt. Apo), *Elmer 11291* (GH–lectotype; A, NY, US–isotypes); Surigao, *Wenzel 3354* (A, GH, NY); Zamboanga Dist., Malangas, *Ramos & Edano 37307* (A).

In both habit and appearance this species is closely allied to *Mussaenda villosa* Wall., of Siam, Malaya, Sumatra, and Borneo. The resemblance is so great that *Clemens 562* from Mindanao was identified by Merrill as *M. villosa*, an error later rectified. Close examination of the collections *Ramos 1836, 1783* (US), etc., of *M. villosa* from British North Borneo, shows that the characters of the Philippine plant are sufficiently distinct for its treatment as a separate species. Both *M. villosa* and *M. scandens* are climbers with elliptic, pubescent leaves, slender flowers in terminal, pubescent cymes, glabrous fruits with deciduous calyx segments and spiny seeds. The flower buds of *M. villosa* are rounded at the top, somewhat constricted at the neck between the corolla tube and the lobes. Its sepals are lanceolate and corolla tube glabrous on the outer surface below the level of the stamens. *Mussaenda scandens* on the other hand bears flower buds which are elliptic at the top and not constricted at the neck. Its sepals are linear-oblong and the corolla tube entirely hairy on the outer surface. The hairs on the leaves of the former are long. *Wenzel 3354* from Surigao differs slightly from the type in its longer sepals and corolla tube. The species may be distinguished from others by its climbing habit, ovate-elliptic or -oblong, pubescent leaves; slender corolla tube pubescent on the outer surface, hairy within 4/5 way down; sharply acuminate, linear-oblong sepals; ovate-acuminate stipules with diverging lobes; glabrous berries with deciduous calyx segments, and spiny seeds with 3 to 9 foveae in the areoles of the testa.

19. **Mussaenda setosa** Merr. Philip. Jour. Sci. Bot. 10: 104. 1915 (TYPE: *Merrill 9496*). FIG. 1, m; FIG. 4, d, e.

Shrub or small tree, 3–4 m. high with terete, pale grayish-brown branches, the younger ones hirsute. Leaves in equal or subequal pairs, oblong-elliptic, elliptic, or ovate, 12–25 cm. long, 6–13 cm. broad, acuminate, rounded or decurrent-acuminate at base, setose on both surfaces, the margins ciliate, lateral veins 15–18 pairs, prominent on the lower surface; petiole 0.5–3 cm. long, hirsute. Stipules ovate, acuminate, 6–8 mm. long, 6.5 mm. broad at the base, bifurcate from apex for about 1/2 their length, lobes subulate, diverging, hirsute on the outer surface, glabrous within except at the base and among numerous glands occurring in 2 groups. Inflorescence a terminal, divaricate, few-flowered, hirsute-ciliate cyme; bracts and bracteoles small, lanceolate, about 3.5 mm. long, hairy on both surfaces, tufted at the base within, bracteoles broader, trifid. Flowers probably heterostylous, subsessile or on stout, pubescent pedicels shorter than the ovaries. Calyx lobes persistent, linear-lanceolate, 4–7 mm. long, 1 mm. broad, hairy on both surfaces with 2 pairs of glands within at the base of each; petaloid sepal white, broadly ovate, 7 cm. long, slightly acuminate, puberulent on the upper surface, hirsute on veins beneath, "petiole" 1 cm. long, hirsute. Corolla tube white, cylindric, 3 cm. long, hairy outside, inside hairy as far as the bases of the anthers, hairs not tufted at the mouth and short in the long-styled forms (short-styled form not seen); corolla lobes yellow, broadly ovate, about 2.5 mm. long, abruptly acuminate, hairy on the outer surface, glabrous within. Stamens with short filaments, epipetalous on the tube a little below the middle in long-styled forms; anthers linear-lanceolate, dorsifixed, introrse, 4.5 mm. long, blunt at the apex and bilobed at the sterile base. Ovary broadly fusiform, setose-ciliate, 2-locular with numerous ovules on axile placentae; style 1.6 cm. long, stigma lobes stout, 7.5 mm. long in the long-styled form. Berry ellipsoid, 1.5 cm. long, sparingly hirsute, black when dry, calyx lobes persisting until nearly ripe.

DISTRIBUTION. This species is endemic to Palawan where it grows on forested ridges at an altitude of about 700 meters. It has been collected in flower in April.

**Philippine Islands.** PALAWAN: Mount Capoas, Malampaya Bay, *Merrill 9496* (US–lectotype), April 1913.

The only specimen available for examination was the isotype from the United States National Museum belonging to the long-styled form and this is chosen as the lectotype, the holotype having been destroyed. The species seems to be distantly allied to *Mussaenda palawanensis* in the stipule and petal characters while differing from it in numerous other characters. It is, however, distinguished from other species by its characteristic setose indumentum, large leaves with 15–18 pairs of lateral veins which are prominent on the lower surface; ovate, bifurcate stipules; long, slender

corolla tubes, and sparingly hirsute, ellipsoid berries with persistent calyx segments.

20. **Mussaenda vidalii** Elmer, Leafl. Philip. Bot. 3: 993. 1911 (TYPE: *Elmer 11309*); Merrill, Enum. Philip. Fl. Pl. 3: 520. 1923.
FIG. 2, q, r, s, t, u, v, w, x.

Scandent shrub or small tree, 3–4 m. tall with lax, somewhat drooping, lenticellate, ferruginous pubescent branches. Leaves ovate, oblong-ovate or elliptic, 9–25.5 cm. long, 4.3–15.2 cm. broad, abruptly acute at apex, broadly obtuse, cuneate or rounded at base, ferruginous hairy on the upper surface, densely so on the lower surface with 6–11 pairs of lateral veins; petiole 1–5 cm. long, hirsute. Stipules deciduous, triangular-lanceolate, 6.5–10.5 mm. long, 6–9 mm. broad at the base, bifurcate from the apex 1/3–1/2 their length, lobes erect or slightly diverging, hirsute on the outer surface, glabrous or scantily hairy within at the base with few or numerous glands. Inflorescence a terminal, dichotomously branched, hairy, many-flowered cyme; bracts and bracteoles linear, or broadly lanceolate, 3–5 mm. long, hairy on the outer surface, glabrous or pubescent within, bracteoles broader, trifid at the apex. Flowers heterostylous on stout, densely hairy pedicels shorter than the ovaries. Calyx lobes oblong or ovate, 4–10 mm. long, 1–3.2 mm. broad, tapering to an acute apex, hairy on both surfaces, hairs on the outer surface longer and more dense; petaloid sepal whitish, 5–10 cm. long, 2.5–8.5 cm. broad, subacute, short cuneate at base, hirsute on both surfaces, 5-veined, "petiole" 2–2.5 cm. long, hirsute. Corolla tube yellowish green, 2.2–3 cm. long, curved, broad above, tapering to a narrow base, densely hairy on the outer surface, hairs long and spreading more or less at right angles to the tube, hairy within as far as the bases of anthers or lower, not tufted at the mouth; hairs extending as far as 1/2 the length of the tube in long-styled forms and 2/5 the length of the tube from the top in short-styled forms; corolla lobes pink to orange-red or yellow, broadly orbicular, 2–3 mm. long, 4–6 mm. broad, abruptly acute, hairy on the outer surface, papillate within. Stamens with short filaments, epipetalous 1/2–2/3 way up on the tube in long-styled forms and 3/5 way up in short-styled forms; anthers linear, dorsifixed, introrse, 5–6.2 mm. long, slightly bent, bilobed at the base. Ovary turbinate, 3.5–5.5 mm. long, densely hairy, 2-locular, with numerous ovules on cushion-shaped, axile placentae; style and stigma lobes 1.7–2.8 cm. and 6–8 mm. long respectively in long-styled forms, 2.5 mm. and 2 mm. long in short-styled forms. Berry ellipsoid, 1.5–2.2 cm. long, ferruginous pubescent, lenticellate, calyx lobes deciduous; seeds minute, reticulate, 0.53–0.73 mm. long, with 3–8 foveae in the areoles of the testa.

DISTRIBUTION. This species grows along the margins of humid forests or in the secondary growth of open rolling country at elevations between 150 and 600 meters above sea level in the islands of Mindanao, Leyte, and Samar. The type collection was made at 1140 meters elevation. Material

has been collected in flower between March and August; in fruit in March, June, and July.

**Philippine Islands.** SAMAR: Catubig River, *Ramos 24485* (A); Loquilocon, *Sulit 6098* (A); Mt. Cansayas, *Sulit 14366* (A); Bagacay, *Sulit 6280* (A). LEYTE: *Wenzel 667* (A); Ormoc, Antilao River, *Edano 11873* (A, PNH); Lake Danao, *Edano 11926* (PNH). MINDANAO: Bukidnon Prov., Pigtaoranan, *Anonuevo 13516* (A, PNH); Tangculan and vicinity, *Ramos & Edano 39050* (A), *39186* (A, US), *39035* (GH, US); Davao Dist., Todaya (Mt. Apo), *Elmer 11309* (GH–lectotype; A, NY, US–isotypes); Mt. Apo, *Clemens 15279* (NY, US).

This species shows the greatest variation in the collections from Leyte. They differ from the type collection in that they are small trees, with broader bracts and bracteoles in the inflorescence, ovate sepals somewhat resembling those of *Mussaenda macrophylla*, broader petals, and larger anthers and fruits. The seeds are identical with those of the typical form both in size and in the number of foveae in the areoles of the testa.

*Mussaenda vidalii* may be distinguished from other species by the spreading, ferruginous pubescence on stems, leaves, and flowers, the oblong or ovate sepals, short petals, large pubescent fruits with deciduous calyx segments, and the small seeds with 2 to 8 foveae in the areoles of the testa.

USES. The water in which the leaves of *Mussaenda vidalii* have been soaked for a few muintes is used as an eye wash; and the macerated leaves are applied to the head to allay drunkenness.

ROYAL BOTANIC GARDENS,
PERADENIYA, CEYLON

# COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XI

## THE XYLEM OF PERESKIOPSIS AND QUIABENTIA

I. W. BAILEY [1]

IT IS OF INTEREST from a taxonomic point of view that *Pereskiopsis* and *Quiabentia* may be differentiated anatomically from *Pereskia* (1) by the characteristic development in young stems of a highly differentiated crystalliferous hypodermis in these genera (Bailey, 1961b); (2) by the absence of diagnostic forms of sclereids in their secondary phloem (Bailey, 1961a); (3) by the sporadic occurrence in their stems and leaves of the curious short cells with broad annular or helical thickenings which have attracted so much discussion in the mammillarias and other excessively succulent forms of the Cactaceae (Bailey, 1960); and (4) except in comparisons with *Pereskia conzattii* Britt. & Rose, *Pereskia autumnalis* (Eichlam) Rose, and *Pereskia nicoyana* Web., by the characteristic pseudopalmate or palmate vasculature of their leaves (Bailey, 1960).

At present uncertainties regarding the status of the numerous described species of *Pereskiopsis* and *Quiabentia* are fully recognized by many taxonomists. Owing to these uncertainties and to the wide ranges of structural variability, not only in the same clone when grown under different environmental influences, but also in different parts of a single adult plant, it seems advisable in a preliminary investigation of the xylem to concern oneself largely with ranges of anatomical variability at a generic level rather than with possible structural differences between putative species and geographical races of the two genera.

The anatomical data presented in the following pages are based upon the investigation of 33 collections of *Pereskiopsis* from various parts of Mexico, kindly preserved for me largely by Norman Boke, R. L. Dressler, Efraim Hernández X., Myron Kimnach, and R. V. Moran. Twenty-nine of these collections exhibited more or less reliable affinities to the following putative species: *P. aquosa* (Web.) Britt. & Rose *three collections*, *P. blakeana* Ortega *two*, *P. chapistle* Britt. & Rose *five*, *P. diquetii* Britt. & Rose *one*, *P. gatesii* Baxter *one*, *P. pititache* Britt. & Rose *three*, *P. porteri* (Brand.) Britt. & Rose *seven*, *P. rotundifolia* (DC.) Britt. & Rose *one*, *P. scandens* Britt. & Rose *one*, *P. spathulata* (Otto) Britt. & Rose *two*, and *P. velutina* Rose *three*. There is no reliable clue at present to the affinities of four other collections.

In the case of *Quiabentia*, I have material of *Q.* aff. *chacoensis* Backbg.

[1] This investigation was financed by a grant from the National Science Foundation. I am indebted to the American Philosophical Society for the loan of a Wild microscope.

collected by Carenzo and Legname in the Jujuy Province of Argentina, of *Q. pereziensis* Backbg. collected by Cárdenas in Bolivia, and of *Q. zehntneri* (Britt. & Rose) Britt. & Rose obtained from a cultivated clone by Boke.

From the point of view of the phylogeny of the dicotyledons as a whole, the cambium and xylem of *Pereskiopsis* and *Quiabentia* have attained a high general level of evolutionary specialization comparable to that which has occurred in *Pereskia* and in a number of dicotyledonous families (Bailey & Srivastava, 1962). The fusiform initials of the cambium are comparatively short and tend to become arranged in stratified or "storied" patterns. The vessel members are short and have simple porous perforation plates; the wood parenchyma strands are short and of scanty paratracheal distribution in denser parts of the secondary xylem; the libriform fibers which may be septate or non-septate function in the storage of starch; and the rays are multiseriate, uniseriate ones having been phylogenetically eliminated. It should be noted in this connection, however, that in *Pereskiopsis*, as at times in *Pereskia*, the vessels which commonly are diffusely distributed either singly or in small clusters frequently exhibit aggregation into concentric zonal patterns in association with varying proportions of wood parenchyma (FIGS. 1–5).

It is in divergent trends of specialization (i.e., *excessive broadening of multiseriate rays and the elimination of secondary walls and lignification within them*) that stems of *Pereskiopsis* and *Quiabentia* differ most significantly from those of most species of *Pereskia*. In the case of arborescent forms of *Pereskia*, incipient evidence of the suppression of lignification, when present, is confined in *P. sacharosa* Griseb., *P. grandifolia* Haw., and *P. bleo* DC. to the innermost part of the first-formed multiseriate rays of roots (Bailey, 1963c). In arborescent forms of *P. colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose, and *P. portulacifolia* Haw., the phenomenon is accentuated in roots but not in stems (Bailey, 1963d). In the arborescent *P. conzattii* Britt. & Rose, *P. autumnalis* (Eichlam) Rose, and *P. nicoyana* Web., it occurs in a curiously modified form in the innermost parts of multiseriate rays in basal parts of large trunks (Bailey, 1963b). In contrast to these larger arborescent forms of pereskias, the smaller commonly more shrubby forms of *P. humboldtii* Britt. & Rose, *P. weberiana* K. Schum., and *P. diaz-romeroana* Cárd., with their not infrequent decumbent, scrambling or scandent branches, exhibit highly accentuated trends of divergent specialization in their roots, but only slight incipient evidence at times of the elimination of secondary walls and lignification in their stems (Bailey, 1963a). Within *Pereskia*, it is the highly scandent *P. aculeata* Mill. which differs most markedly from other species in having advanced trends of divergent specialization in both its roots and stems (Bailey, 1962).

In contrast to the arborescent species of *Pereskia*, the numerous putative species of *Pereskiopsis* are relatively low plants of shrubby form with stems or branches which frequently tend to be more or less decumbent, scrambling, or scandent. It should be noted that collectors find it difficult at present to locate plants of unmodified form in the wild. In many cases

specimens are obtainable only from plants cultivated in hedges or gardens, or, in remoter regions, from plants that have been cut back or variously mutilated by the activities of man. However, in all investigated collections, the ranges of variability in width, distribution, and internal structure of the multiseriate rays are extensive in stems from different parts of a single plant or clone. Furthermore, in the larger stems of all putative species of *Pereskiopsis*, there are conspicuous evidences of divergent trends of structural specialization, i.e., those leading toward more or less extensive elimination of secondary walls and lignification in rays and wood parenchyma.

In parts of some stems of *Pereskiopsis*, the first-formed secondary xylem resembles the wood of *Pereskia sacharosa* and of other arborescent pereskias. In such dense tissue (FIG. 1) comparatively narrow multiseriate rays, related to parenchymatous gaps of the eustele, are fully lignified, and relatively uniformly distributed as seen in transverse sections (FIGS. 1 and 3). In subsequently formed secondary xylem (FIGS. 3 and 4) the broadening rays exhibit more or less extensive patches of unlignified tissue which contain abundant druses of calcium oxalate. In addition, more or less extensive arcs or zones of unlignified wood parenchyma are of common occurrence (FIGS. 4 and 5) not infrequently in association with zonal aggregations of vessels (FIG. 5).

In other stems of *Pereskiopsis*, having broader parenchymatous gaps in the eustele, the rays of the first-formed secondary xylem are broader (compare FIGS. 3 and 9). The inner parts of such rays, related to interfascicular parts of the eustele, may be lignified, or unlignified (as in FIG. 9). Furthermore, in such rays the cells frequently are broader tangentially than radially. In subsequently formed secondary xylem, more or less extensive patches of unlignified ray tissue and unlignified zonal wood parenchyma tend to occur (FIG. 7).

In transverse sections of some stems, aggregations of excessively broadened, lignified, unlignified, or partly unlignified rays may occur in wedges of secondary xylem which alternate around the circumference of a stem with intervening wedges of wood of denser, more normal structure, i.e., having narrower rays and a higher proportion of lignified vessels and libriform fibers. In these stems, the denser precociously flaring wedges of secondary xylem are related internally to the fascicular parts of the eustele. Such structural tendencies are diagrammatically illustrated in FIG. 2, a transverse section of a stem of *Pereskiopsis porteri*. In this stem, there are five conspicuous wedges of softer secondary xylem that are depressed below the outer boundary of denser, structurally more normal, intervening ones. The number of depressed wedges in the transverse section of the stem suggests a possible correlation with a 2/5 or 3/8 phyllotaxy.

That aggregations of broadened rays actually are related to phyllotaxy may be demonstrated by examining decorticated stems after treatment with phloroglucin-HCl (TEXT-FIG. B), or by studying tangential longitudinal sections of the secondary xylem. As shown in the case of *Pereskiopsis* aff. *aquosa* (FIGS. 11 and 12), the connecting vascular tissues of the

leaf and areole are subtended in the secondary xylem by broad unlignified rays and relatively few tenuous strands of lignified libriform fibers and vessels. In passing downward from such a node through successively lower internodes to the next node of an orthostichy, the rays sooner or later become narrower and the strands of intervening lignified libriform fibers and vessels become correspondingly more numerous and broader. Thus, the structural differences between wedges of secondary xylem, visible in transverse sections of these stems, are due largely to the level at which the orthostichies are sectioned below their nodes.

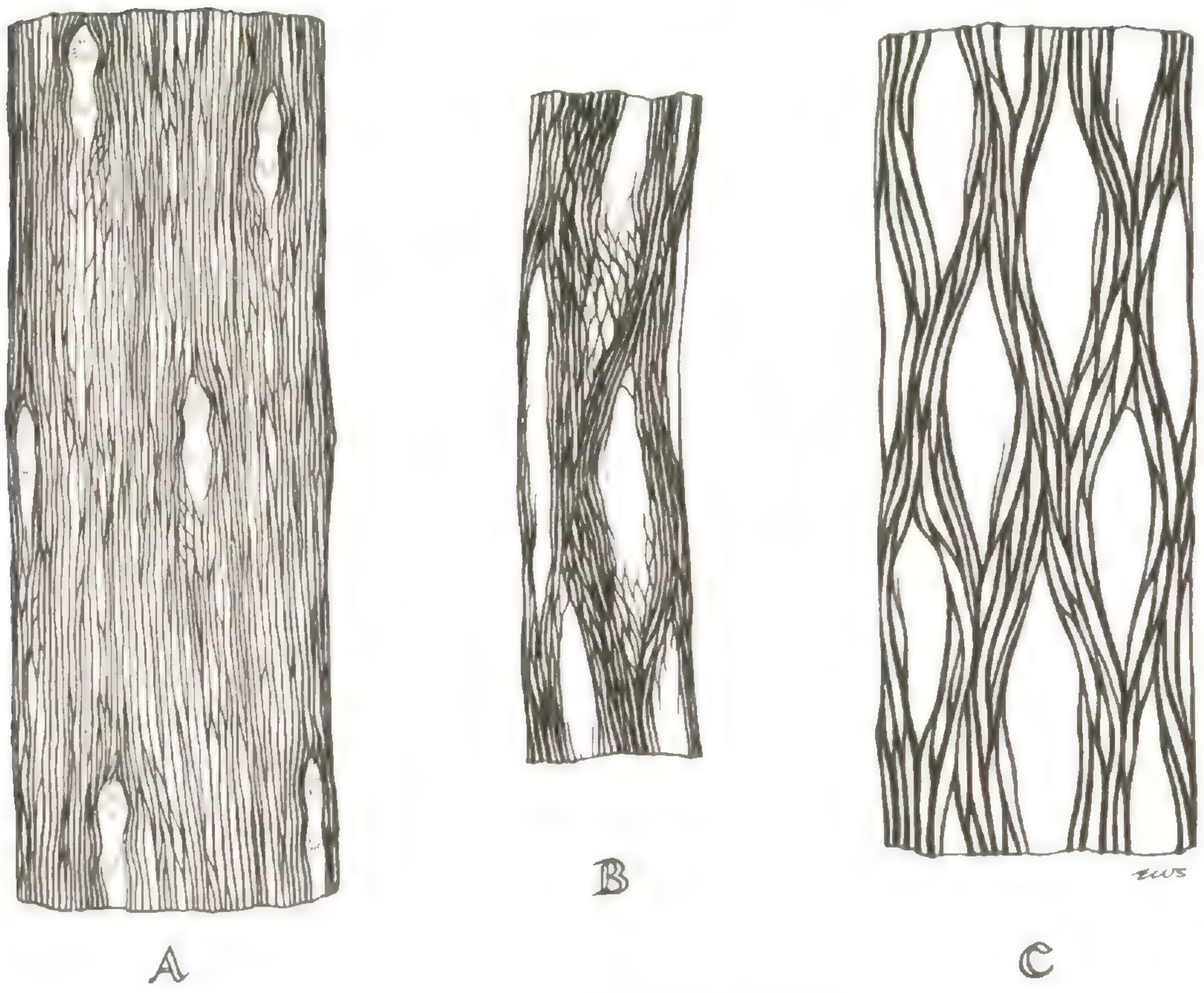
In some larger stems of *Pereskiopsis* aff. *aquosa* the aggregations of multiseriate rays subtending the node of an orthostichy, not only are very broad and unlignified as in FIG. 12, but also at times tend, just below the node, to fuse forming a broad wedge of unlignified tissue as seen in transverse sections (FIG. 13). In such wedges of unlignified parenchyma, narrow strands of lignified libriform fibers and vessels may be eliminated, their place being occupied by more or less vertically elongated, unlignified derivatives of the cambium between the broad fusing rays (FIG. 13).

It should be emphasized that in *Pereskia* the connecting vascular tissues of the leaves and areoles are jacketed in the secondary xylem by a very limited amount of unlignified parenchyma and are subtended by fully lignified tissue. When decorticated the stems resemble TEXT-FIG. A, except that the rays are lignified throughout their radial extension outward in the secondary xylem.

In the case of *Pereskiopsis*, some stems exhibit comparable lignification in the earlier formed secondary xylem. In other stems or parts of stems, lignification tends to be suppressed in the secondary xylem for varying distances below the connecting vascular tissues of the leaves and areoles (TEXT-FIG. B).

In basal parts of some of the largest stems of *Pereskiopsis* aff. *aquosa*, cells with broad annular thickenings occur, not only in elements of the primary body adjacent to vessels of the fascicular parts, but also in unlignified multiseriate rays of the secondary xylem. In the primary body, the cells are more or less elongated vertically and of fusiform outline (FIG. 16), and have more than one annular thickening per cell. In the rays of the secondary xylem, on the contrary, the cells are of rectangular form and contain a single broad annular thickening per cell (FIGS. 15 and 17).

The xylem in roots of *Pereskiopsis* commonly exhibits divergent trends of anatomical specialization comparable to those that occur in roots of *Pereskia aculeata* (Bailey, 1962), *P. cubensis*, and *P. portulacifolia* (Bailey, 1963d). The inner parts of multiseriate rays related to protoxylem poles of the primary body tend to be unlignified. In the outward extension of these rays, and in those subsequently formed, there tend to be alternating patches of lignified and unlignified tissue. In addition, more or less extensive arcs or zones of unlignified wood parenchyma are of not infrequent occurrence. However, in general, the divergent tendency toward suppression of lignification tends to be more highly accentuated in stems than in roots of *Pereskiopsis*. This is in contrast to what happens in most species




TEXT-FIGS. A–C. Decorticated stems treated with phloroglucin-HCl, natural size. A, *Quiabentia* aff. *chacoensis* [Tucuman], B, *Pereskiopsis porteri* [*Moran 7349*], C, *Quiabentia zehntneri* [*Boke*].

of *Pereskia* where incipient trends of divergent specialization commonly are more advanced in roots than in stems.

In an earlier paper of this series (Bailey, 1961b), I noted briefly that where crystals of calcium oxalate are deposited in the fully lignified rays of arborescent pereskias, they occur as single large crystals or a few smaller independent ones, aggregations into typical druses being absent. Conversely, where multiseriate rays or parts of them are unlignified, druses of calcium oxalate are conspicuously developed. Since writing this paper additional collections of roots and stems of *Pereskia* and *Pereskiopsis* have been obtained. Although conspicuously numerous druses occur characteristically in unlignified ray tissue of these collections, minor aberrations may occur at times in rays that are composed of alternating patches of lignified and unlignified tissue. For example, in the case of *Pereskia colombiana* and *P. guamacho*, where single large crystals are unusually abundant in the lignified rays of stems, a few crystals of this form may occur in association with druses in unlignified patches of ray tissue in roots. Conversely, a few druses may occur at times in lignified parts of the rays in stems of *Pereskiopsis*. Most exceptional in this connection, however, is the occurrence of a few druses in the fully lignified rays of stems of the Peruvian and Bolivian pereskias.

According to descriptions and illustrations in the literature, *Quiabentia*

*chacoensis*, *Q. pereziensis* and *Q. zehntneri* are characterized by their erect stems bearing a number of upstanding coarse branches from which relatively short smaller ones diverge. All of the aerial parts of these plants (stems, branches, and leaves) are highly succulent. In my limited collections of the three species, the stems and larger branches have a greatly expanded pith and a relatively much reduced volume of secondary xylem. For example, in a stem of *Q. pereziensis* six centimeters in diameter, the pith has a breadth of three centimeters; in a stem of *Q.* aff. *chacoensis*, having a diameter of three and one half centimeters, the pith is two centimeters in diameter; and in a vigorous branch of *Q. zehntneri*, having a diameter of three centimeters, the pith is 18 millimeters in breadth.

It should be emphasized in this connection, however, that the accentuated succulence in stems and branches of *Quiabentia* is not due solely to excessive expansion of the soft tissues of the primary body with concomitant reduction in cambial activity. There is an obvious tendency in the secondary xylem, as in many stems of *Pereskiopsis*, toward increasing the proportion of unlignified tissue and concomitantly reducing the proportion of lignified libriform fibers and vessels. As indicated in FIG. 10, part of a transverse section of a vigorously growing branch of *Q. zehntneri*, the conspicuously broadened multiseriate rays are unlignified and contain numerous druses of calcium oxalate. This is true even in wedges of secondary xylem that are subtended by fascicular parts of the eustele and results in the formation of relatively widely spaced, exceedingly narrow wedges of lignified tissue composed of libriform fibers and vessels (compare FIG. 10 and TEXT-FIG. C.)

A similar tendency toward reduction of lignification occurs in stems of *Quiabentia pereziensis*. In FIG. 8, part of a transverse section cut near the base of a large stem, i.e., nearer the level of the ground, the narrower strands of secondary xylem are less diagrammatically distributed, being contorted by irregularities in the grain of the wood. Furthermore, they contain patches of unlignified wood parenchyma as well as lignified libriform fibers and vessels. The contortions of the grain and the excessive breadth of the unlignified rays in this stem are shown in tangential longitudinal section in FIG. 14.

The stems of *Quiabentia pereziensis* and *Q. zehntneri* in my limited collections, when decorticated and treated with phloroglucin-HCl, have conspicuous unlignified parenchymatous lacunae in the secondary xylem subtending the leaves and areoles at nodal levels (TEXT-FIG. C), as in some stems of *Pereskiopsis* aff. *aquosa* and *P. porteri* (TEXT-FIG. B). In the case of *Quiabentia* aff. *chacoensis*, the only stem of comparable diameter available to me at present has relatively long internodes and broad wedges of lignified xylem between its unlignified multiseriate rays, i.e., as seen in transverse sections of the stem. Furthermore, although there is some tendency for aggregation of broadened rays in the secondary xylem subtending the bases of the leaves and areoles at subnodal levels (TEXT-FIG. A), these rays do not fuse to form large conspicuous unlignified parenchymatous lacunae comparable to those that occur in secondary xylem

of *Q. pereziensis* and *Q. zehntneri*. This suggests that the tendency toward increasing succulence of the wood in *Quiabentia* is less advanced in *Q.* aff. *chacoensis* than in the other two species of the genus. The suggestion is strengthened by the structure of one available root of *Q.* aff. *chacoensis*. As illustrated in FIG. 6, the xylem is of normal fully lignified structure and closely resembles that which occurs in the roots of *Pereskia sacharosa* (Bailey, 1962, Fig. 2) and other dicotyledons at equivalent levels of phylogenetic anatomical specialization. However, until extensive collections become available for studying the ranges of structural variability in different plants of the same clone or species, conclusions regarding anatomical differences between putative species of *Quiabentia*, as between those of *Pereskiopsis*, must remain largely tentative.

## SUMMARY AND GENERAL CONCLUSIONS

Evidence presented in this and preceding papers reveals incipient stages of divergent anatomical specialization in *Pereskia*, *Pereskiopsis* and *Quiabentia*. One of the most significant of these, for a clearer understanding of greatly accentuated succulence in stems of the Opuntieae and Cereeae, is the tendency toward increasing the circumference of the eustele with concomitant expansion of the pith during later ontogenetic stages of the development of the primary body. Incipient stages of this phenomenon are detectable in larger immature stems of various pereskias (Bailey, 1962, 1963c, 1963d). In such stems expansion of the parenchymatous interfascicular parts of the eustele and enlargement of the pith may occur after initiation of cambial activity in fascicular parts of the primary body. Enlargement of the pith is much accentuated in the basal parts of the large trunks of *Pereskia conzattii*, *P. autumnalis*, and *P. nicoyana* (Bailey, 1963b). In these pereskias, multiseriate rays related to unlignified parenchymatous gaps of the eustele remain unlignified and their cells have a capacity for tangential expansion, thus facilitating additional increase in the circumference of the eustele and enhanced enlargement of the pith. As indicated in this paper, similar phenomena are of commoner occurrence in stems of *Pereskiopsis* and *Quiabentia* (FIGS. 7, 9, and 10).

However, as indicated earlier in this paper, enhanced succulence in stems of *Quiabentia* and *Pereskiopsis* is not due solely to increasing the proportion of soft tissue in the primary body, with concomitant reduction in the volume of secondary xylem. There is obvious evidence of divergent trends of specialization in the secondary xylem itself, leading to increasing succulence by suppression of secondary walls and lignification in multiseriate rays and wood parenchyma. Although this phenomenon is largely confined in *Pereskia* to roots and to stems of the scandent *P. aculeata*, it becomes more or less highly accentuated in stems of *Pereskiopsis* and *Quiabentia*. Furthermore, there is a tendency in some stems of the latter genera for aggregations of broad unlignified rays to subtend the connecting vascular tissues of leaves and areoles at nodal levels. This phenomenon is particularly significant in attaining a clearer understanding of the origin and

development of huge parenchymatous lacunae in the secondary xylem of various representatives of the Cereeae and Opuntieae. The breadth, longitudinal extension, and structural details of such subtending succulent strands of secondary xylem vary more or less markedly at times even in different stems of the same clone or plant. Many of the more conspicuous structural differences appear to be correlated at least in part with variations in the diameter of the primary body, in the number of fascicular strands in the eustele, in the width of parenchymatous gaps between them, with changes in phyllotactic patterns from 2/3 to 3/8 and possibly to 5/13, and with variations in vigor of growth involving conspicuous differences in internodal elongation.

There are additional trends of divergent anatomical specialization that merit attention. One of these is the tendency to form zones of wood parenchyma as seen in transverse sections of stems. Such zonal patterns of wood parenchyma commonly are associated with concentric aggregations of vessels and appear to be correlated with seasonal variations in cambial activity and in the maturation of cambial derivatives. Although zonal aggregations of vessels and *lignified* wood parenchyma occur in the later-formed secondary xylem of large stems of several arborescent pereskias, incipient stages of the *suppression* of lignification in wood parenchyma of stems is largely confined in *Pereskia* to the scandent *P. aculeata*. In contrast to this, the suppression of lignification in wood parenchyma is of common occurrence in stems of the shrubby representatives of *Pereskiopsis* and *Quiabentia*.

A trend of divergent specialization, which does not occur in any of my numerous collections of *Pereskia*, is the sporadic occurrence in leaves and stems of *Pereskiopsis* and *Quiabentia* of the curious short cells with broad annular or helical thickenings which are so abundantly developed in more succulent representatives of the Cactaceae. The occurrence, distribution, and structure of these cells in *Pereskiopsis* and *Quiabentia* merit additional detailed investigation, since the study of more comprehensive collections of adequate material may yield clues regarding the origin, function, and phylogenetic significance of such curious cells in the Cactaceae as a whole.

It should be emphasized in conclusion that in the leaf-bearing Cactaceae accentuations of divergent trends of anatomical specialization are more or less closely associated with changes in the stature and habits of growth of the plants in which they occur. In arborescent forms of *Pereskia* (i.e., those having a more typically woody dicotyledonous habit of growth) incipient stages of divergent specialization in the xylem are rarely detectable in *P. sacharosa*, *P. grandifolia*, and *P. bleo*; more or less conspicuous in roots of *P. colombiana*, *P. guamacho*, *P. cubensis*, and *P. portulacifolia*; and confined in *P. conzattii*, *P. autumnalis*, and *P. nicoyana* to the first-formed secondary xylem in the basal parts of large trunks of the trees. On the contrary, the phenomena are greatly accentuated in roots of the comparatively low, shrubby forms of Peruvian and Bolivian pereskias, and in both roots and stems of the scandent *P. aculeata*. In contrast to this, all stems in available collections of the shrubby representatives of *Pereskiopsis* and

*Quiabentia*, regardless of variations in their habit of growth and in different degrees of succulence, exhibit more or less accentuated divergent trends of specialization in their xylem. Thus, the various representatives of *Pereskia*, *Pereskiopsis*, and *Quiabentia* may be arranged in an ascending evolutionary series of increasing divergent specialization. In this ascending phylogenetic sequence, the arborescent forms of *Pereskia* occur at the lowest level and the highly succulent forms of *Quiabentia* at the apex. Furthermore, the evolutionary series at least suggests that among surviving representatives of the family *Pereskia sacharosa*, *P. grandifolia*, and *P. bleo* have most closely retained the vegetative habit of growth and internal structure of ancestral Cactaceae.

From a purely taxonomic point of view, the structure of the xylem provides additional diagnostic criteria for differentiating *Pereskia* from the genera *Pereskiopsis* and *Quiabentia*. However, it does not at present provide a convincing argument for separating *Rhodocactus* from *Pereskia* or *Pereskiopsis* from *Quiabentia*.

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———. 1963d. X. The xylem of *Pereskia colombiana*, *Pereskia guamacho*, *Pereskia cubensis*, and *Pereskia portulacifolia*. *Ibid*. **44**: 390–401.

——— & L. M. SRIVASTAVA. 1962. Comparative Anatomy of the leaf-bearing Cactaceae. IV. The fusiform initials of the cambium and the form and structure of their derivatives. *Ibid*. **43**: 187–202.

## EXPLANATION OF PLATES

(The black spots in unlignified tissue of FIGS. 2–4, and 9–13 are druses. Those in FIG. 14 are starch.)

## PLATE I

FIGS. 1 & 2. Transverse sections of stems, 1, *Pereskiopsis* aff. *chapistle* [*Boke B-3*], inner xylem of a vigorously growing shoot 25 millimeters in diameter with a pith six millimeters in diameter, × 14. 2, *Pereskiopsis porteri* [*Moran 7349*],

part of a stem 18 millimeters in diameter with a pith three millimeters in diameter, × 11.

## PLATE II

FIGS. 3 & 4. Transverse sections of stems. × 11. 3, *Pereskiopsis* aff. *chapistle* [*Boke B-3*], inner part of a stem seven centimeters in diameter with a pith four millimeters in diameter. 4, *The same*, part of outer secondary xylem.

## PLATE III

FIGS. 5 & 6. Transverse sections of secondary xylem, × 11. 5, Part of outer xylem from the same stem as FIGS. 3 & 4. 6, *Quiabentia* aff. *chacoensis*, section of a root.

## PLATE IV

FIGS. 7 & 8. Transverse sections of xylem, × 11. 7, *Pereskiopsis* aff. *aquosa* [*Dressler*], section of basal part of stem six centimeters in diameter with a pith eight millimeters in diameter. 8, *Quiabentia pereziensis* [*Cárdenas*], large root.

## PLATE V

FIGS. 9 & 10. Transverse sections of stems, × 11. 9, *Pereskiopsis* aff. *aquosa* [*Dressler*], xylem from a stem four centimeters in diameter with a pith 12 millimeters in diameter. 10, *Quiabentia zehntneri* [*Boke*], part of xylem from a stem four centimeters in diameter with a pith 14 millimeters in diameter.

## PLATE VI

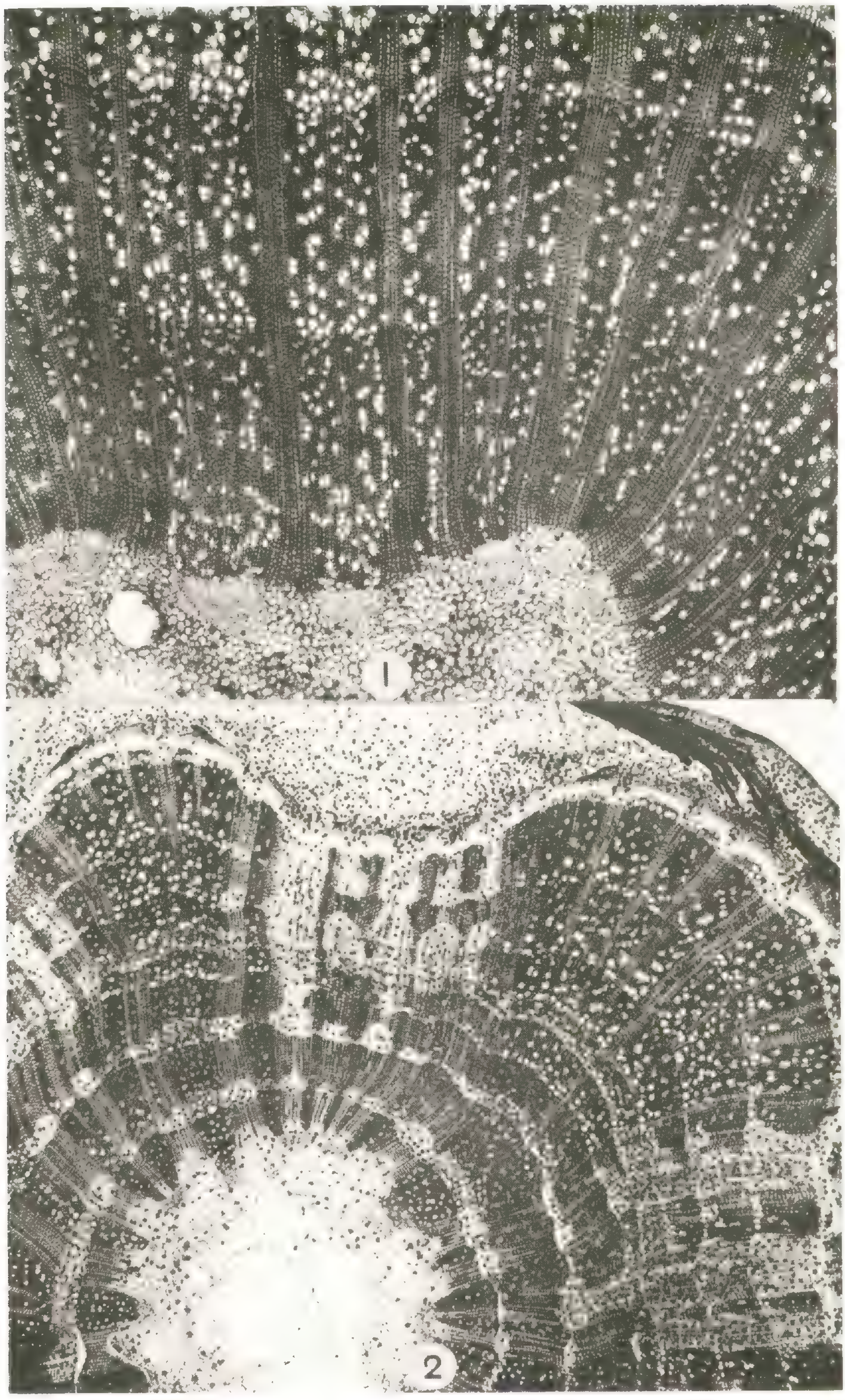
FIGS. 11 & 12. Tangential longitudinal sections of stems of *Pereskiopsis* aff. *aquosa* [*Boke B-31*], × 7. 11, From a stem 23 millimeters in diameter with a pith seven millimeters in diameter, showing leaf traces and cylindrical vascular tissue of areole. 12, From a stem five centimeters in diameter with a pith nine millimeters in diameter.

## PLATE VII

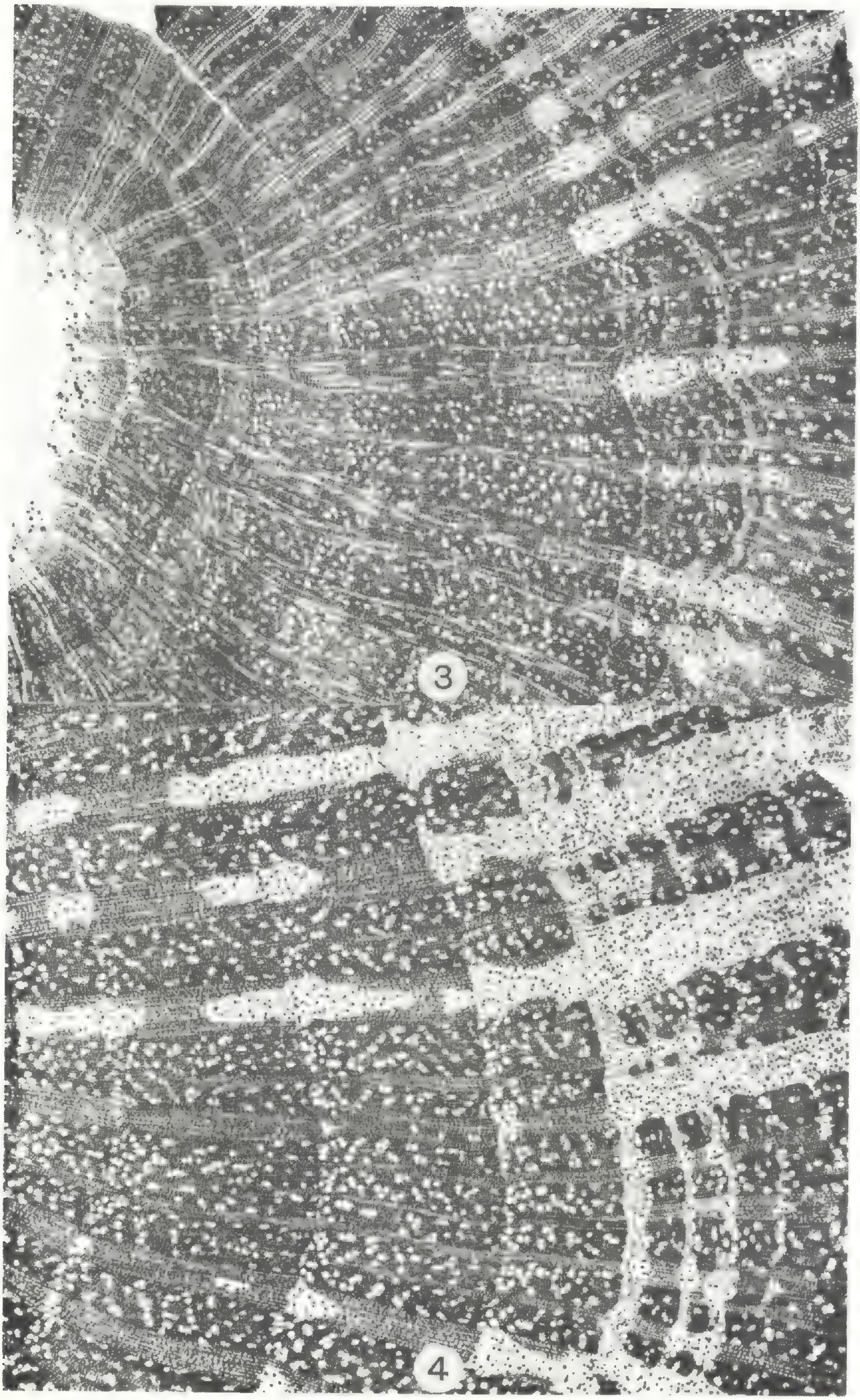
FIGS. 13 & 14. Transverse and tangential longitudinal sections. 13, *Pereskiopsis* aff. *aquosa* [*Boke B-31*], transverse section of larger stem, × 7. 14, *Quiabentia pereziensis* [*Cárdenas*], tangential section of outer secondary xylem from a stem six centimeters in diameter with a pith 33 millimeters in diameter, × 43.

## PLATE VIII

FIGS. 15–17. Sections from the largest basal part of a stem of *Pereskiopsis* aff. *aquosa* [*Dressler*], × 88. 15, Transverse section of ray cells showing broad annular thickenings. 16, Longitudinal section of the outer part of the eustele showing fusiform cells with broad annular thickenings. 17, Radial section of a multiseriate ray showing single broad annular thickening in ray cells.




BAILEY, LEAF-BEARING CACTACEAE, XI

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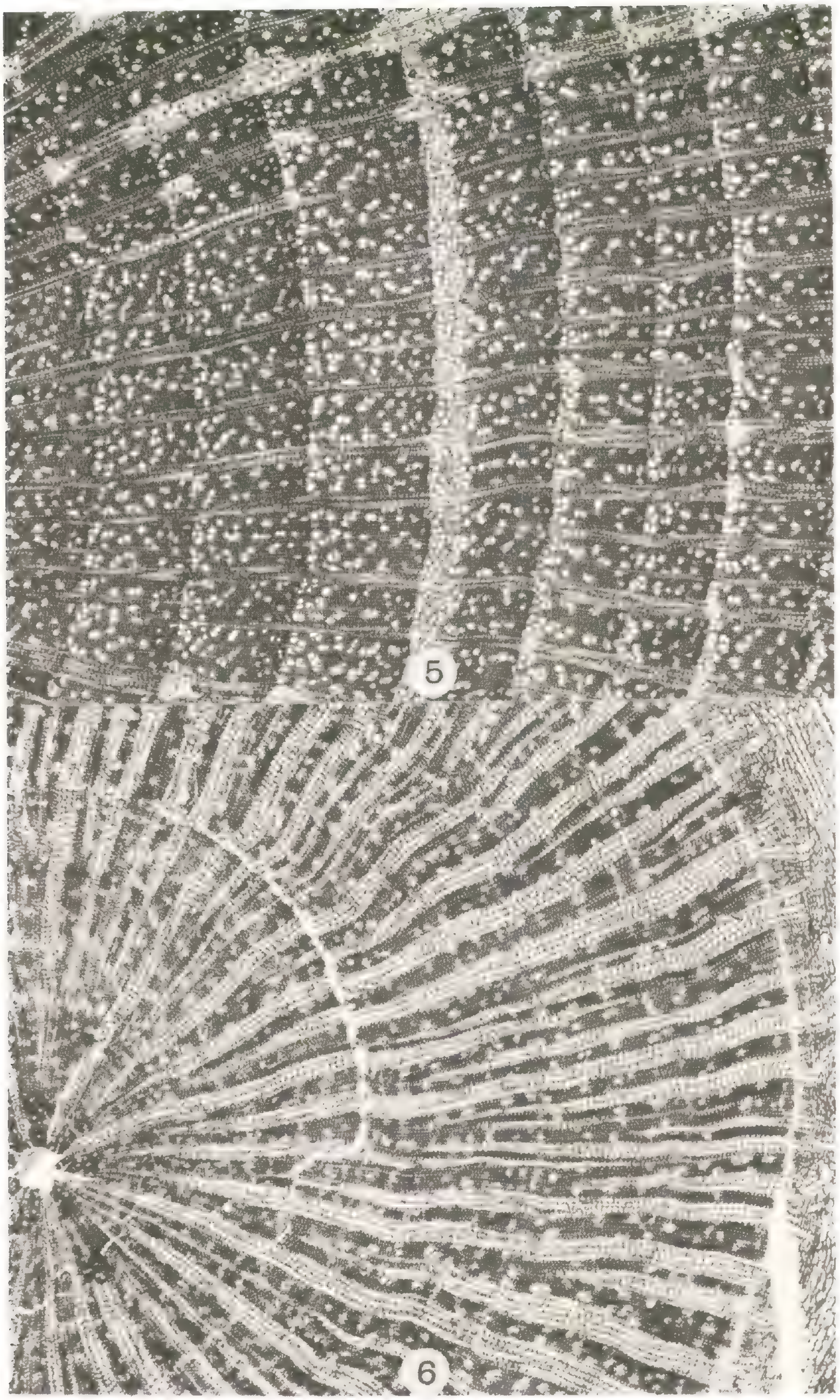


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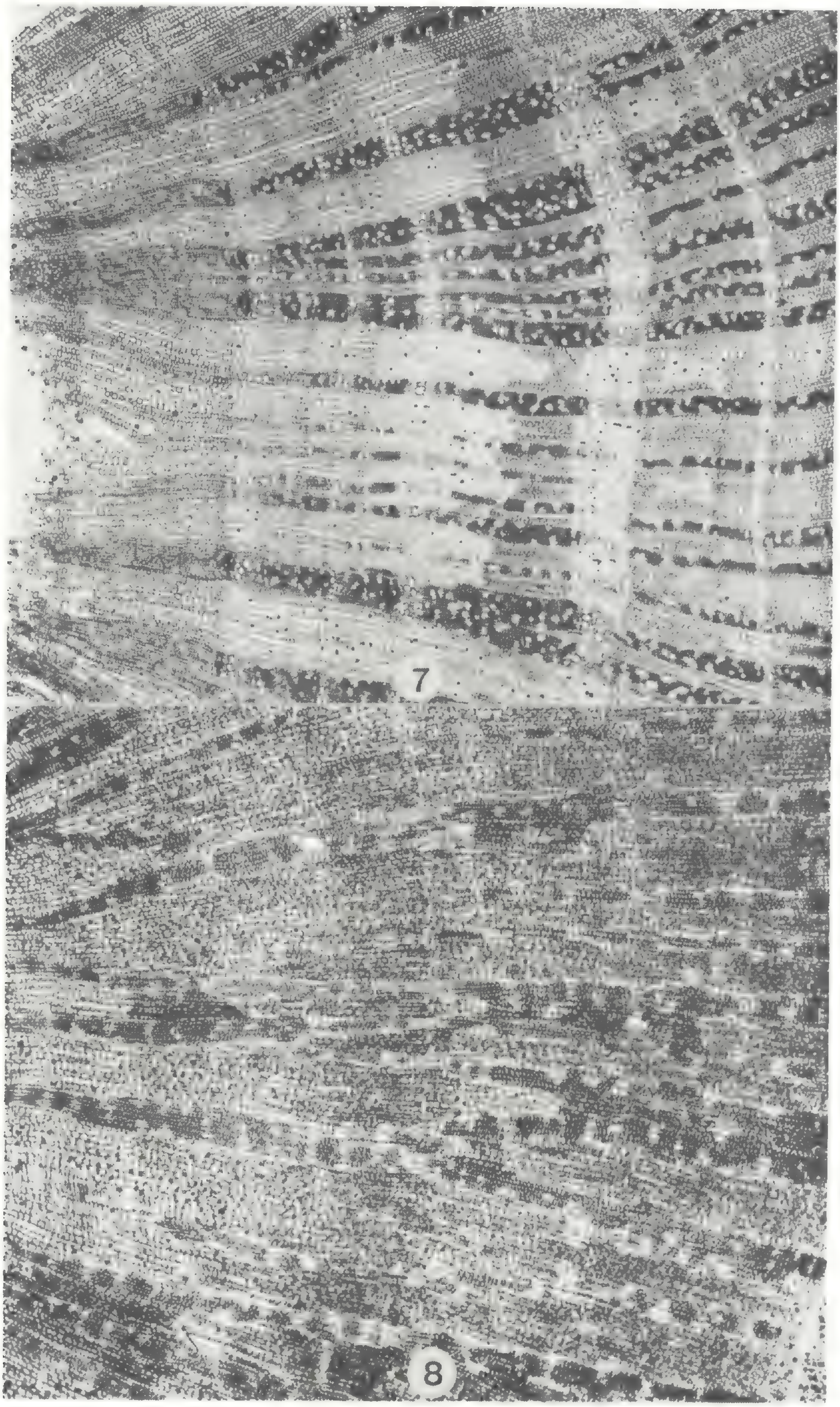


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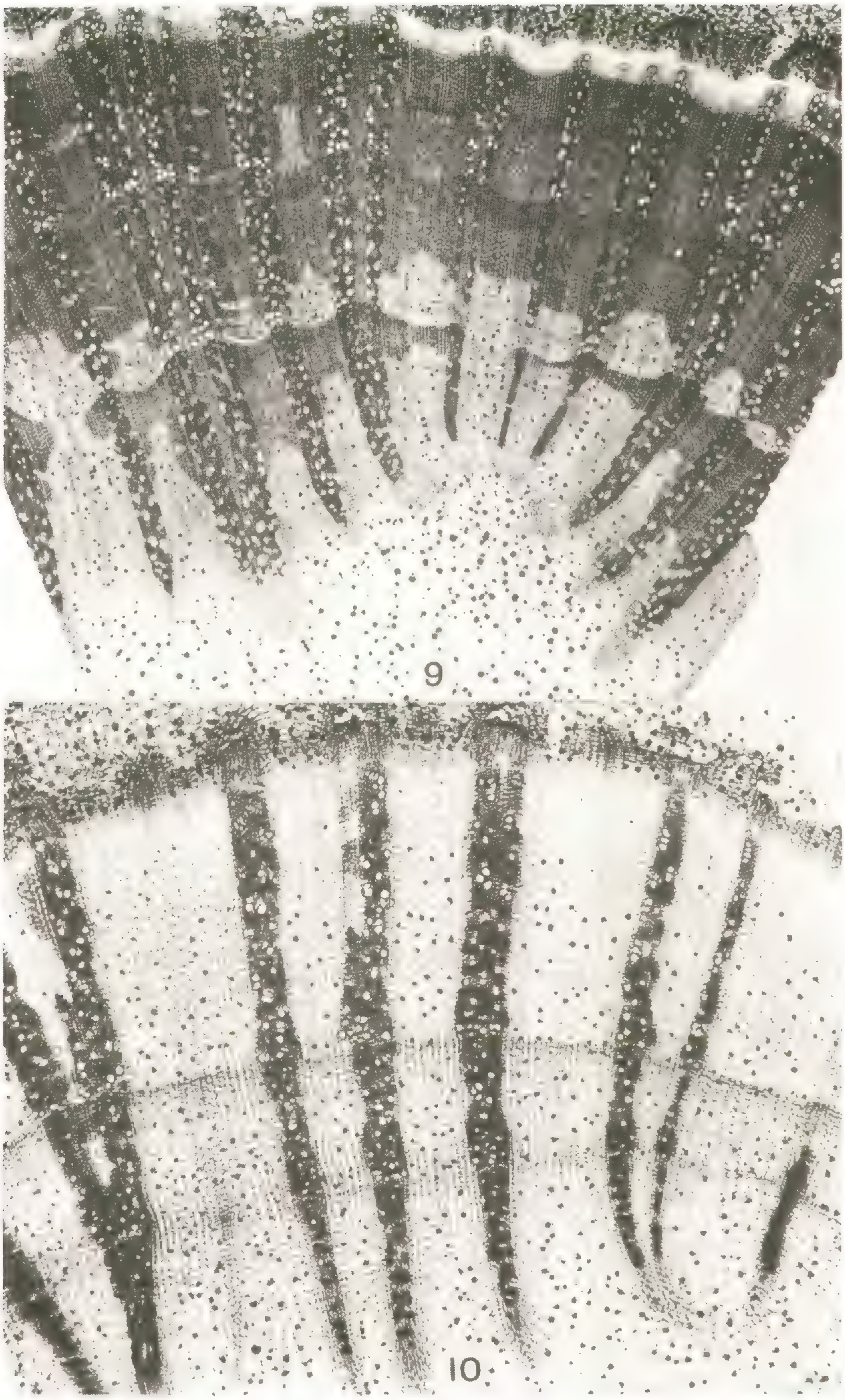


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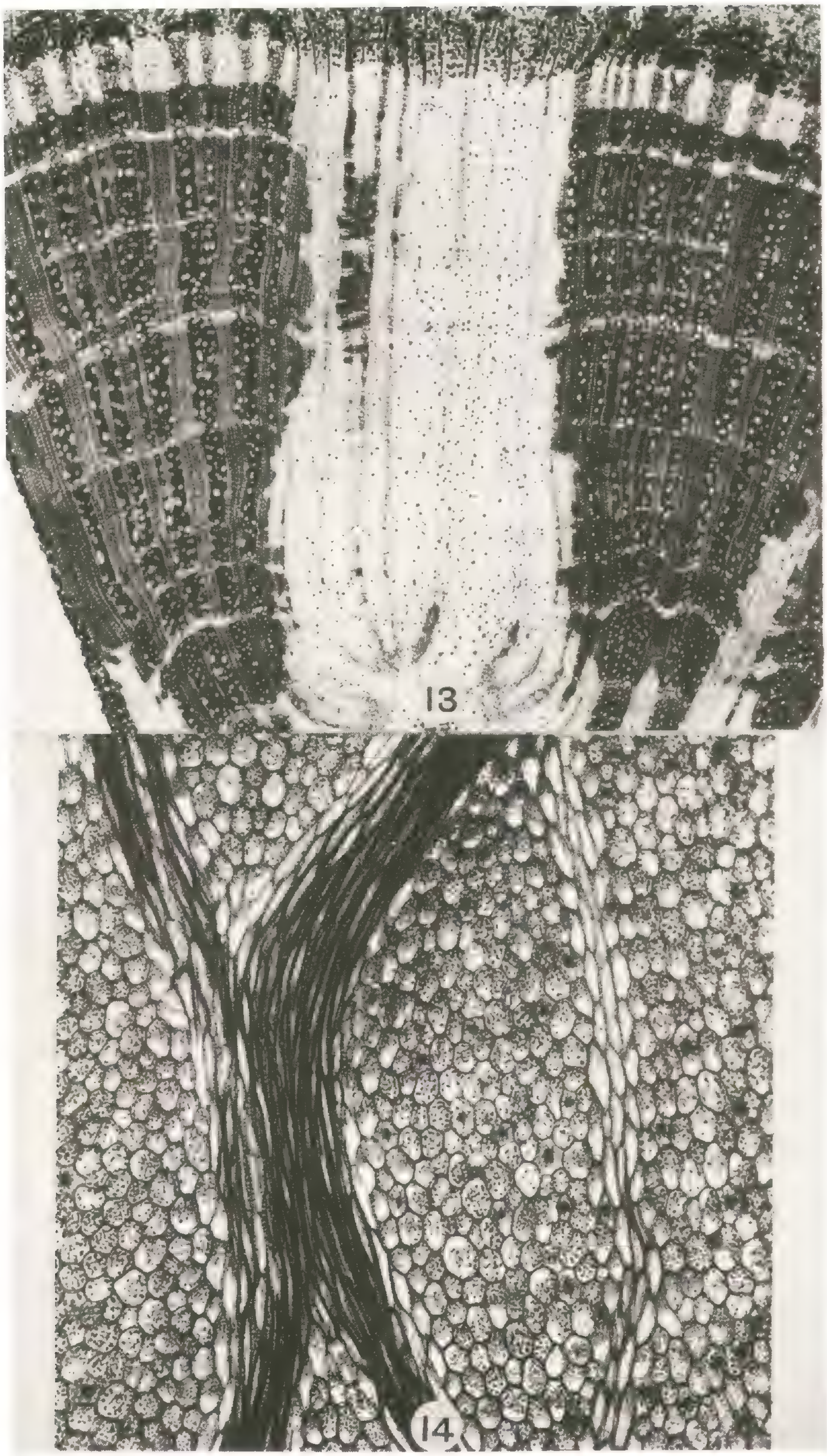
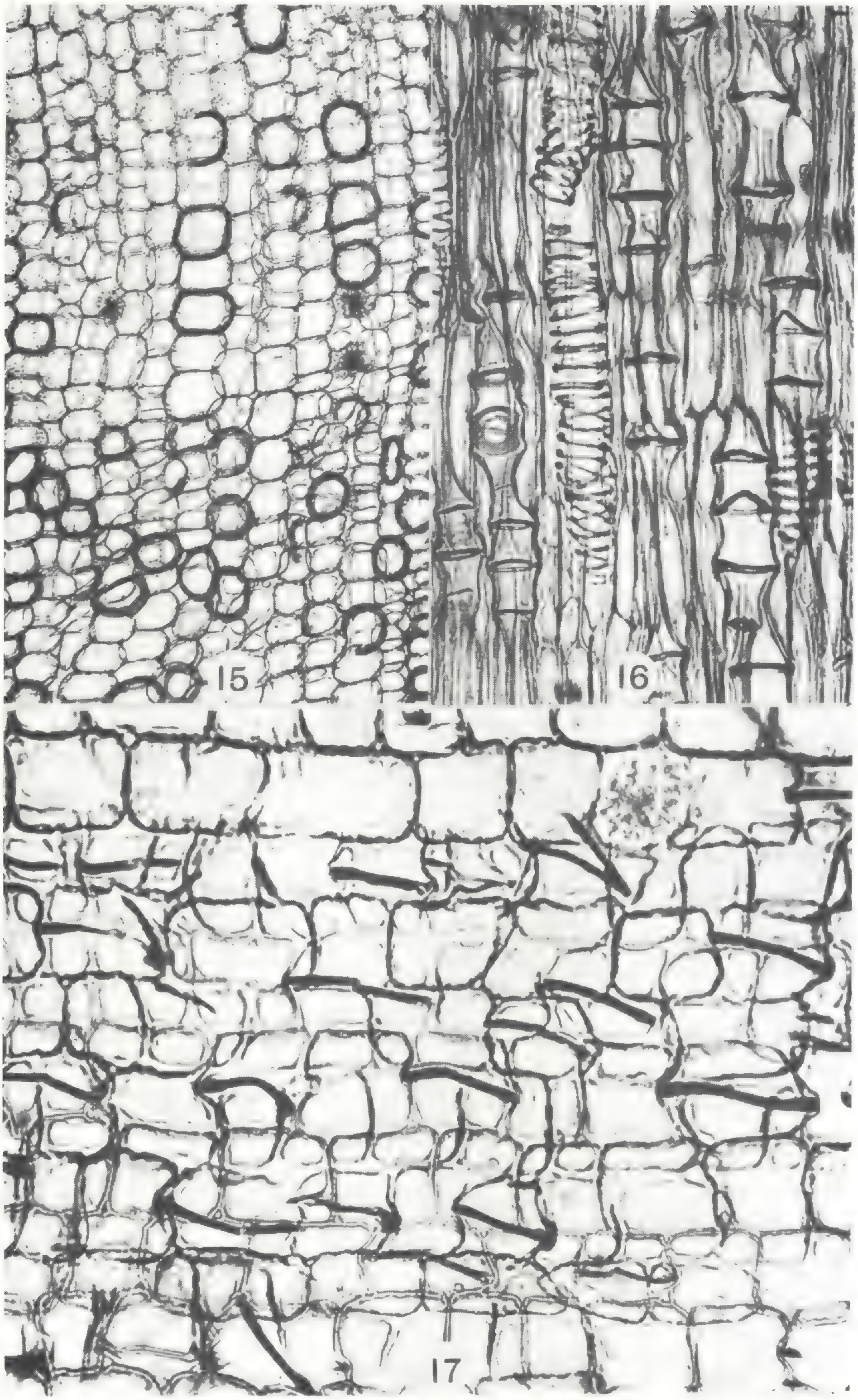



BAILEY, LEAF-BEARING CACTACEAE, XI




BAILEY, LEAF-BEARING CACTACEAE, XI

# TYPIFICATION IN DIRCA

LORIN I. NEVLING, JR.

IN THE THYMELAEACEOUS GENUS *Dirca* L., which is restricted to Canada and the United States, two species, *D. palustris* L. and *D. occidentalis* Gray, are known. *Dirca palustris* has an extensive range in eastern North America; *D. occidentalis* is restricted to six counties in California. It is of interest that there has been no taxonomic confusion in the genus since it was described as a *Thymelaea* by Gronovius in 1743 (*Flora Virginica* 155), and there has been only one nomenclatural synonym for the genus during this period, which presents no problem, being based directly on *Dirca* L. (*Dofia* Adans. Fam. 2: 285. 1763). Although with this virtually unblemished history the question of typification has never been of critical importance, there are some interesting aspects concerning typification of the two species which seem worth discussing.

The type species of the genus, *Dirca palustris*, was described, validly, by Linnaeus in *Species Plantarum* (358. 1753) with the citation "palustris. 1. Dirca *Gen. Nov.* 1078.*," the asterisk indicating that in the volume cited there was a good description. The citation refers to *Nova Plantarum Genera* . . . Leonhard Johan Chenon, 1751, one of a long series of dissertations written by Linnaeus but defended, as theses, by his students. In both the dissertation and the *Species Plantarum* the description of *Dirca palustris* is taken verbatim from Gronovius' *Flora Virginica* (155. 1743), and from this description alone it is impossible to tell whether or not Linnaeus had actually seen the plant described. In the dissertation, under *Dirca*, Linnaeus cited "fig. 7.," but in the two copies of it which I examined the figures were lacking. In his *Genera Plantarum* (ed. 4. 167. 1754) Linnaeus again used Gronovius' description for *Dirca*. In 1756, the portion of the Linnaean dissertation of 1751 concerning *Dirca* was republished (Linn. Amoen. Acad. ed. 1. 3: 12, 13). Here the description of Gronovius is repeated once more, but Linnaeus also provided an original diagnosis and an illustration of a flowering branchlet and inflorescence (presumably the same as "fig. 7." of the dissertation). The illustration of the flowering branchlet agrees reasonably well with specimen no. 501.1 in the herbarium of the Linnean Society of London. The sheet apparently was seen by Linnaeus before 1753 and bears the handwritten notation "1. palustris." It is listed by B. D. Jackson (Index to the Linnean Herbarium in Suppl. Proc. Linn. Soc. London, 124th Sess., 26, 69. 1912) as being present in the herbarium of Linnaeus in 1753. Specimen number 501.1 must, therefore, be considered the holotype rather than a specimen Gronovius might have had, in spite of the number of times Linnaeus chose to repeat the Gronovian description. According to

the citation of Gronovius of 1743 the plants he examined for *Flora Virginica* were collected by John Clayton. In the edition of *Flora Virginica* of 1762 (p. 60) the citation "Clayt. n. 858." is appended to the description of *Dirca palustris*. In addition, Linnaeus (see Jackson *ibid.* 11) is quoted as saying, "When I assisted Dr. Gronovius in examining plants from Virginia I got Duplicates of most of them." The holotype specimen in the Linnean Herbarium (LINN) is very likely of Clayton's collecting and given by Gronovius to Linnaeus.

The first report of *Dirca* in California was published by John Torrey in 1857 (Botany, in Reports of Exploration and Surveys **4**: 133). This reference is to *D. palustris* L. in which Torrey says, "Mountains near Oakland, California; April 4, (with flowers and young fruit.) We have never before received this plant from any part of the United States west of the Mississippi." *Dirca palustris* is now well known as far west as eastern Oklahoma but Torrey's reference can only be to the plant later described by Asa Gray (Proc. Am. Acad. **8**: 631. 1873) as *D. occidentalis*. The collection of April 4, 1854, from Oakland, was made by Dr. J. M. Bigelow and has been cited by some as the holotype (McMinn, H. E. *Manual of California Shrubs* p. 365. 1951) which it clearly is not. Gray, following his description of *D. occidentalis*, and remarking on the Bigelow collection says, "there are only vestiges of the former [the flowers and young fruit] in my specimens. If they had been in good condition, Dr. Torrey would have noticed the characters of the species, which are now manifest." The additional specimen making the characters "manifest" is "Dr. A. Kellogg & W. G. W. Harford n. 895 of distribution." This collection was made March 13, 1869, in the Oakland hills. Both the Bigelow and Kellogg & Harford collections are mounted on a single sheet now on deposit in the Gray Herbarium (GH). On this sheet are three branchlets with the left-hand (immature fruit) and center specimens (sterile ? and insect damaged) comprising the Bigelow collection while the right-hand specimen (flowering) is the Kellogg & Harford gathering. The Bigelow label contains only the name "Dirca" while the Kellogg & Harford label bears, in Gray's handwriting, "Dirca occidentalis n. sp. A. G." Therefore, there is little question that the latter, and later, collection should be considered the holotype of *D. occidentalis*.

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# THE GENUS CHAENOMELES (ROSACEAE)

CLAUDE WEBER

THE JAPANESE OR FLOWERING QUINCE, botanically, the genus *Chaenomeles* of the family Rosaceae, has been under cultivation in temperate areas of the world for over 400 years. Selections have been made and named in nearly every country where the plants are grown. Through the years, horticulturists have selected and propagated over 500 named varieties (cultivars). The classification of these many cultivars has been difficult, for unresolved problems exist in the morphology and taxonomy of the plants at the generic, specific, and varietal levels. Individual species exhibit a plasticity of form which is troublesome to botanists but of value in commercial horticulture. Hybrids are known involving two or all three species of the genus in both simple and in multiple crosses.

One of the goals of this study was to determine whether such a large group of cultivars of woody plants, largely of unknown parentage, could be placed in a systematic arrangement. The late L. H. Bailey, in his *Manual of Cultivated Plants*, did not attempt to include the cultivated varieties of *Chaenomeles*. He stated "To describe the main varieties of cultivated plants, even those customarily meriting Latin names, requires long and painstaking study, collections for the most part not in existence, historical perspective, a special application of nomenclature, and an appreciation of systematic values yet little developed." I have tried in the present study to meet these qualifications.

The Arnold Arboretum has an excellent representation of the common cultivars of *Chaenomeles* in its living collections. Through the cooperation of many other botanical gardens and commercial nurseries, representatives of most available cultivars were assembled for comparative studies. Directors and curators of herbaria and arboreta in many parts of the world have graciously loaned or given herbarium specimens of *Chaenomeles* species, varieties, and cultivars, and these have been an important aid in the historical and descriptive studies of the genus. The taxonomic, floristic, and horticultural literature in many libraries has supplied an "historical perspective." Of particular value in assembling the hundreds of "fancy names" applied to the selections of Japanese Quinces has been

the collection of nursery catalogues of the Massachusetts Horticultural Society. The "special application of nomenclature" and the "appreciation of systematic values" which Bailey pointed out were "little developed" in 1948, have both matured with the acceptance of the category of "cultivar" in the 1953 and subsequent editions of the *International Code of Nomenclature for Cultivated Plants*.

The genus *Chaenomeles* comprises only three species of moderate-sized shrubs adaptable to cultivation in temperate areas. By observing the plants through several years the seasonal changes in morphology could be observed; growing them in close proximity or in isolation, the natural and man-induced breeding habits could be studied. Collections of fruits, seeds, cuttings, and scions allowed experimentation on methods of germination, propagation, and subsequent development.

Living plants were the subject of this study when current observations could be compared with the descriptions published in a scattered supporting literature, and with an assemblage of herbarium specimens. Regrettably, a study of the basic species in China and Japan has not been possible and the known ecology of *Chaenomeles* is that of the plants in cultivation.

The taxonomic study of the genus *Chaenomeles* would have been impossible without examining numerous specimens dispersed in the herbaria of North America, Europe, and Asia. I wish to thank the directors and curators of the following institutions for the loan of herbarium specimens. They are cited according to the standard abbreviations of *Index Herbariorum*.

A Arnold Arboretum of Harvard University, Cambridge, Massachusetts
AAH Herbarium of cultivated plants, Arnold Arboretum, Jamaica Plain, Massachusetts
BM British Museum (Nat. Hist.), London, England
G Conservatoire et Jardin Botaniques, Genève, Switzerland
GH Gray Herbarium of Harvard University, Cambridge, Massachusetts
K Herbarium, Royal Botanic Gardens, Kew, Surrey, England
L Rijksherbarium, Leiden, Netherlands
LE Botanical Institute of the Academy of Sciences, U.S.S.R., Leningrad, U.S.S.R.
NY New York Botanical Garden, New York
P Muséum National d'Histoire Naturelle, Paris, France
US U. S. National Museum, Smithsonian Institution, Washington, D. C.
TI Botanical Institute, University of Tokyo, Hongo, Tokyo, Japan
UPSV Växtbiologiska Institutionen, Uppsala Universitet, Uppsala, Sweden

Among the historical herbarium specimens, the "cultivars" were little represented. To fill this gap, numerous persons sent fresh material or took the time to press flowering branches, and to compile data. To the staffs of the following arboreta and nurseries, goes my appreciation for the gifts of living plants and herbarium specimens which added to both the living collection and the herbarium of cultivated plants of the Arnold Arboretum in Jamaica Plain, Massachusetts:

Beal-Garfield Botanic Garden, East Lansing, Michigan
Belmonte Arboretum, Wageningen, Netherlands
Dawes Arboretum, Newark, Ohio
Department of Parks, Rochester, New York
Du Pont Arboretum, Winterthur, Delaware
George Landis Arboretum, Esperance, New York
Holden Arboretum, Mentor, Ohio
Ida Cason Callaway Gardens, Pine Mountain, Georgia
Longwood Gardens, Kennett Square, Pennsylvania
Morris Arboretum, Philadelphia, Pennsylvania
Morton Arboretum, Lisle, Illinois
Mount Airy Arboretum, Cincinnati, Ohio
New York State Agricultural Experiment Station, Geneva, New York
New York Botanical Garden, New York
Orland E. White Arboretum, Boyce, Virginia
Planting Fields Arboretum, Oyster Bay, New York
Proefstation, Boskoop, Netherlands
Royal Botanic Gardens, Kew, Surrey, England
Stanley M. Rowe Arboretum, Cincinnati, Ohio
Station of Medicinal Plants, Kasukabe-Shi, Japan
Tudor House, Ripley, England
United States National Arboretum, Washington, D. C.
United States Dept. of Agriculture, Plant Introduction Station, Glenn Dale, Maryland
University of Connecticut, Storrs, Connecticut
University of Washington Arboretum, Seattle, Washington
Villa Taranto, Verbania-Pallanza, Italy
Bunyard Nursery, Maidstone, England
Darthuizer Nursery, Leersum, Netherlands
Fruitland Nursery, Augusta, Georgia
Harrison Nursery, New Zealand
Monrovia Nursery, Azusa, California
Phytotektor, Winchester, Tennessee
Wayside Gardens Nursery, Mentor, Ohio
Willis Nursery, Ottawa, Kansas

The staff of the Chinese-Japanese Library of Harvard University was most helpful in checking Chinese and Japanese bibliographical notes or geographic names. The work necessary for the completion of this study was rendered pleasant by the interest and the kindness of the staff of the Arnold Arboretum in Cambridge, Jamaica Plain, and Weston, and of many graduate students in botany, who shared their knowledge or provided any help which was needed. My thanks go especially to Dr. Donald Wyman for sharing his observations on ornamental shrubs, and to Mr. Alfred Fordham for the care he took in propagating material, sometimes received in poor condition. Their horticultural experience was invaluable.

My deepest appreciation goes to Dr. Richard A. Howard, who first suggested the genus *Chaenomeles* as a thesis subject, and whose enthusiasm never failed to be inspiring during the pursuit of this study.

## SYSTEMATIC POSITION OF CHAENOMELES IN THE MALOIDEAE

The genus *Chaenomeles* Lindley is assigned to the subfamily Maloideae [1] of the family Rosaceae. This natural division, under the name Pomaceae was suggested as a "fragmentum" by Linnaeus in 1763, who listed under it several genera such as *Pyrus* and *Crataegus*, but included also *Punica* and *Ribes* which are now placed in the Punicaceae and in the Saxifragaceae respectively. No description was given at that time. Since then, the justification for this taxon has not been contested by taxonomists. Some have treated the Maloideae as a separate family,[2] others as a tribe.[3] Currently it is widely accepted as a subfamily of the Rosaceae.[4]

The morphological characteristics of the Maloideae are: Trees or shrubs, unarmed or spiny. Leaves petiolate, alternate, simple or compound, with free stipules (at least on young shoots). Flowers regular, hermaphrodite (rarely unisexual by abortion), solitary, fasciculate or in terminal racemes, white, pink or red. Calyx campanulate-urceolate with 5 persistent or deciduous lobes. Petals 5, unguiculate, inserted in the throat of the calyx. Stamens 10–60, inserted at the same level as the petals, filaments free, anthers introrse with 2 locules. Disc laminate or fleshy, dry or nectariferous. Ovary formed of (1) 2–5 carpels, more or less adherent to the calyx on their abaxial side, completely fused with it at maturity. Ovules anatropous, usually 2 (1 by abortion) in each locule, to indefinite (*Chaenomeles*, *Cydonia*). Styles 1–5, terminal, free or connate at the base. Pollen tricolpate. Fruit fleshy, usually a pome (exceptionally a berry), formed of the hypanthium, the carpels becoming chartaceous or cartilaginous, and sometimes dehiscing on the adaxial suture, to bony and indehiscent. Seeds ascending (or horizontal when numerous), testa coriaceous, or less often mucilaginous, raphe and chalaza apical (or subapical), endosperm lacking, embryo orthotropous with short and conical radicle and imperceptible plumule.

According to Metcalfe and Chalk (1950), the Maloideae can not be separated by anatomical characters from the other subfamilies of the

[1] According to the *International Code of Botanical Nomenclature*, the name Pomoideae, in current use, is incorrect as it is not based on a genus. The subfamily name Pomoideae should be replaced by Maloideae, based on *Malus* Miller.

**Maloideae** Weber, stat. nov. Type: *Malus* Miller.

*Malaceae* Small, Fl. Southeast. U.S. 529. 1903.

[2] Pomaceae: Lindley, 1822, 1847; Bartling (Pomacées), 1830; Spach, 1834; Meisner, 1836–43; Endlicher, 1841; Walpers, 1843; Hoffmann, 1846; Roemer, 1847; Decaisne, 1874; Dippel, 1893; Burgerstein, 1896a & b, 1898a & b. Malaceae: Small, 1903, 1905; Bessey, 1915.

[3] Pomoideae: Jussieu, 1789. Pomaceae: De Candolle, 1825. Pomeae: Bentham & Hooker, 1865.

[4] Pomeae: Gray, 1842; Koehne, 1893. Pomoideae: Focke, 1894; Dalla Torre & Harms, 1900–07; Ascherson & Graebner, 1906–10; Rendle, 1925; Wettstein, 1935; Diels, 1936; Skottsberg, 1940; Rehder, 1949; Lawrence, 1951; Benson, 1957; Emberger, 1960.

Rosaceae. The genera of the Maloideae have few characteristics in common, as is true in the other subfamilies of the Rosaceae. Variation in the stem structure occurs even in individual species of *Chaenomeles* comparable to that recorded by Aubertot (1910) in the genera *Pyrus*, *Crataegus*, and *Prunus*. The Maloideae (except *Osteomeles*) have exclusively solitary vessels, while most of the other Rosaceae have a tendency to have a few together. They have fibers with fewer bordered pits on the tangential wall than on the radial walls, while the other Rosaceae, except some species of *Spiraea* have pits equally numerous on both walls. The only leaves with glandular teeth are found in *Chaenomeles*, *Pyrus*, *Sorbus*, and *Crataegus*, all members of the Maloideae.

If the Maloideae do not stand apart anatomically from the other subfamilies of the Rosaceae, the genera do so cytologically. According to Sax (1931, 1932, 1934) the basic chromosome number is 17 in all genera of the Maloideae, while it is 8 and 9 in the Spiraeoideae, 7 and 9 in the Rosoideae, 8 in the Prunoideae. This has been confirmed by all subsequent authors, Moffett (1931), Darlington (1945), Delay (1950–51), Cave (1958, 1959, 1960) and Löve and Löve (1961). Only *Quillaja brasiliensis* Mart., which undoubtedly belongs (by its morphology) to the subfamily Spiraeoideae, and has always been placed there by botanists, presents an exception by having 17 pairs (Bowden, 1945). Polyploidy occurs in the whole family Rosaceae, being limited to tri- and tetraploidy in the Maloideae. Darlington and Moffett (1930) suggested that the 17 pairs of chromosomes in *Pyrus* are made up from a basic number of 7 by duplication of 4 pairs and a triplication of 3 pairs of chromosomes. Sax (1932) rejected this idea and proposed that the Maloideae originated by hybridization of members of two different subfamilies, most likely belonging to the Spiraeoideae and to the Rosoideae. The Maloideae would thus be allotetraploid.

In geographic origin, the Maloideae are nearly restricted to the northern temperate hemisphere. Sax (1931) notes that 15 of the 18 genera enumerated by Rehder (1927) are represented by Asiatic species. He concluded that the Maloideae must have originated in Asia before starting their migration toward America (1 genus *Osteomeles* in Hawaii), Europe (1 genus *Chamaemeles* localized in Madeira), and North Africa. Only *Hesperomeles* reached South America, following the Andes as far as Chile.

There is no argument among taxonomists about the genera to be included or excluded from the Maloideae. Difficulty arises, however, when one has to determine the limits of the genera of the Maloideae, for many intergeneric hybrids are reported.

The genera recognized by Rehder (1949) are the following: *Amelanchier* Medicus, *Aronia* Medicus, *Chaenomeles* Lindl., *Cotoneaster* Ehrhart, *Crataegus* L., *Cydonia* Miller, *Docynia* Decaisne, *Eriobotrya* Lindl., *Malus* Miller, *Mespilus* L., *Osteomeles* Lindl., *Peraphyllum* Nuttall, *Photinia* Lindl., *Pyracantha* Roemer, *Pyrus* L., *Rhaphiolepis* Lindl., *Sorbus* L., *Stranvaesia* Lindl. To these should be added the genus *Chamaemeles* Lindl. and *Hesperomeles* Lindl. which are not cultivated, and the hybrid

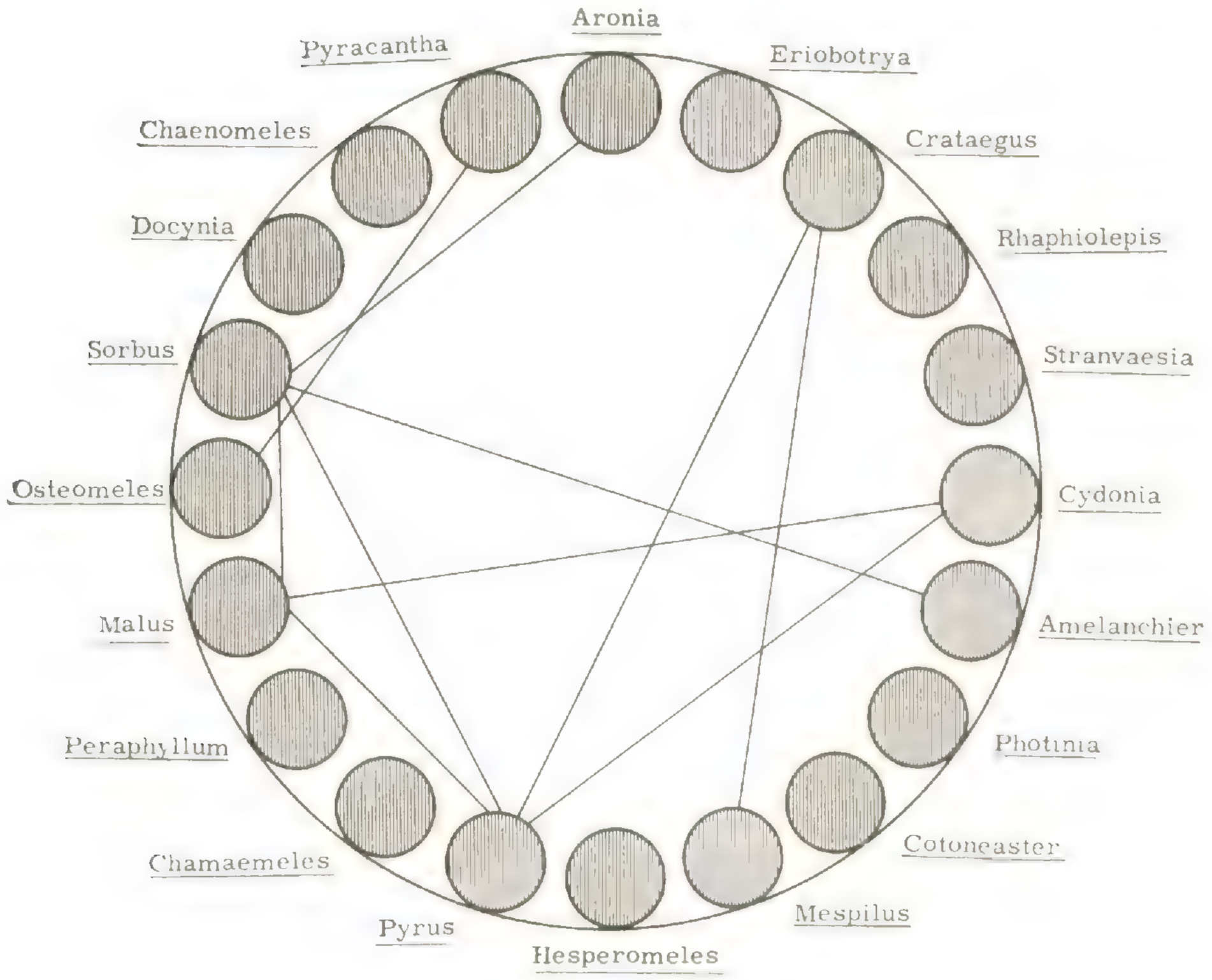


FIG. 1. Sexual intergeneric hybrids in the Maloideae. The genera are not arranged according to their affinities as such an arrangement would make the plate difficult to read.

genera *Amelasorbus* Rehder (*Amelanchier* × *Sorbus*), *Crataegomespilus* Simon-Louis (*Crataegus* × *Mespilus*), *Pyracomeles* (*Osteomeles* × *Pyracantha*), *Pyrocrataegus* Daniel (*Crataegus* × *Pyrus*), *Pyronia* Veitch (*Cydonia* × *Pyrus*), *Sorbaronia* Schneider (*Aronia* × *Sorbus*), *Sorbopyrus* Schneider (*Pyrus* × *Sorbus*). According to Rehder (1940), the cross *Cydonia oblonga* × *Malus* is reported to have been raised by I. V. Michurin, while Sax (in litt.) mentioned that the cross *Malus* × *Pyrus* was produced in Australia (FIG. 1).

Within the subfamily Maloideae, the genus *Chaenomeles* is most closely related to the genus *Cydonia*, with which it shares the character, unusual in the Maloideae, of an indefinite number of seeds in each locule. *Cydonia* and *Chaenomeles* have been placed in the same genus, namely *Cydonia* Miller, by numerous authors.[5] By others, *Chaenomeles* is considered a

[5] Persoon (1807), Loiseleur-Deslongchamps (1815, 1817), Sweet (1818, 1827), Hayne (1822), Guimpel, Otto & Hayne (1825), Siebold (1830), Loudon (1838), Endlicher (1840), Miritzi (1845–46), Van Houtte (1849), Planchon (1849), Lemaire (1856), Verschaffelt (1856) Courtin (1857), Hoffman & Schultes (1864), Wenzig (1874; *Chaenomeles*, 1883), Moore (1875), Nicholson (1884), Goldring (1888, 1891), Frahm (1898), Palibin (1898), Engler & Diels (1900), Ito (1900), Rehder (1900; *Chaenomeles*, 1914), Burgerstein (1901), Hemsley (1901a & b), Schumann (1901), Muth (1902), Bean (1903, 1914, 1930; *Chaenomeles*, 1951), Grignan (1903), Veitch (1903–04), Beckett (1907, 1909–10), Makino (1908), Nakai (1908, 1909; *Chaenome-*

section of *Cydonia*.[6] *Chaenomeles* is also related to *Pyrus*, and to *Malus* if this taxon is separated from *Pyrus*. *Chaenomeles japonica* (Thunb.) Lindl. ex Spach, the type species of the genus, was described first by Thunberg (1784) as a species of *Pyrus*. As late as 1902, some authors still joined *Chaenomeles* (and *Cydonia*) to *Pyrus*.[7] Andrews (1807) transferred *Pyrus japonica* Thunb. to *Malus*.




FIG. 2. Affinities between the genera closely related to *Chaenomeles*. The size of the circle is in proportion to the importance of the genus. The characters indicated between parentheses occur occasionally, or in a minority of the species. The characters given odd numbers are considered more primitive than those having even numbers.

*les*, 1916a), Mottet (1917), Cardot (1918), Richards (1923), Späth (1930), Diels (1936), Faulkner (1941), Hurley (1948), Jex-Blake (1950), Emberger (1960).

[6] De Candolle (1825), Don (1832a), Focke (1894).

[7] Thunberg (1784), Murray (1784), Vitman (1789), Willdenow (1800), Sims (1803), Jacquin (1809), Aiton (1811), Loddiges (1821, 1829), Sprengel (1825), Morris (1826), Morren (1851), Miguel (1867), Koch (1869), Franchet & Savatier (1873–75;

Another closely related genus, *Docynia*, shares with *Chaenomeles* the character of numerous stamens in two rows (40–60 in *Chaenomeles*, 30–50 in *Docynia*). The type species of the taxon, *Docynia indica* (Colebrooke) Decne., was described first as *Pyrus indica* by Colebrooke (in Wallich, 1831), then transferred to *Cydonia* by Spach (1834), before Decaisne (1874) established the genus *Docynia*.[8]

The genus *Pseudochaenomeles* Carrière (1882), based on an unreliable fruiting characteristic of *Chaenomeles japonica* (Thunb.) Lindl. ex Spach (as *C. maulei*) as opposed to *C. speciosa* (Sweet) Nakai (as *C. japonica*), was not maintained by its author. The genus *Pseudocydonia* Schneider, which was first established as a section of *Chaenomeles* by Schneider in May 1906, was raised by him to generic rank in November of the same year, to include *Cydonia sinensis* (Dum.-Cours.) Thouin, will not be considered here. These two genera are not at present recognized by any taxonomist.

In FIGURE 2 an attempt is made to show the affinities between the genera related to *Chaenomeles*. The characters chosen are arranged to offer an alternative. The one given the odd number is supposed to be more primitive than the character having an even number. If it were possible to show the entire subfamily Maloideae on a multidimensional system, it would help to understand the generic limits and the phylogeny of the group. This is not practical for the genera are too numerous and many are not known well enough at the present time.

Because of the wide divergence of opinion among taxonomists as to how many genera should be recognized in the Maloideae, it is presumptuous to attempt to discuss the evolution of the different genera without having studied the whole group carefully. From its geographic distribution, as shown above, from the morphological characters of the inferior ovary and the syncarpic fruit, and from a consideration of the high basic chromosome number, the subfamily Maloideae appears to be of more recent origin than the other subfamilies of the Rosaceae.

The Maloideae is closest morphologically to the Spiraeoideae and the Rosoideae, and closest anatomically to the Prunoideae. The genera of the Maloideae are closely related, as shown by their morphology, and supported by the graft compatibilities (FIG. 3) and numerous sexual hybrids. This was shown by Decaisne in 1872, and Sax in 1931, each of whom wrote that botanists having a tendency for lumping could go as far as to consider all the Maloideae one genus. Burgerstein (1896a) suggested on the basis of the anatomical structure: "Alle untersuchten Pomaceen — 130 Arten (inclusive Hybriden und Varietäten) — die sich auf 16 Gattungen

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Franchet in *Chaenomeles*, 1883), Hemsley (1873; *Cydonia*, 1901), Kurz (1873), Masters (1874a), Neumann (1875), Smith (1875), Hooker (1884), Tanaka & Ono (1891), Arnott (1902).

[8] Abnormal flowers of *Chaenomeles speciosa* observed in the spring of 1961 had the styles fused in a hairy cone protruding above the insertion of the stamens and petals, very much like *Docynia*, and in the extreme cases, no ovules were present. Lobed leaves, frequent in *Chaenomeles* seedlings occur regularly in juvenile leaves of *Docynia indica*.

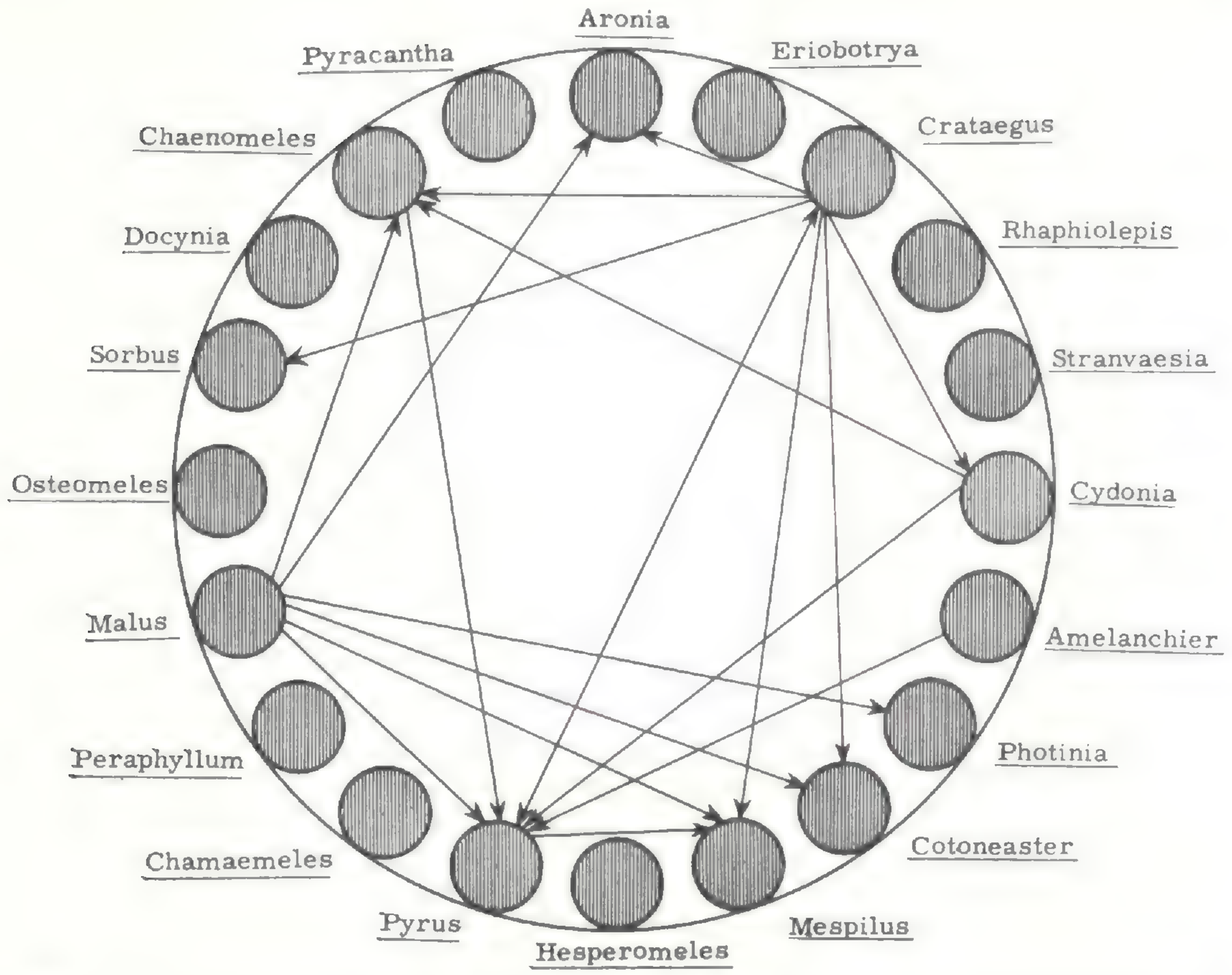


FIG. 3. Grafting affinities of the Maloideae. The arrows indicate the direction from understock to scion.

vertheilen, zeigten im Wesentlichen einem Uebereinstimmenden Holzbau." The genera of the Maloideae are thus delimited mostly for the sake of convenience, and there will always be disagreement among taxonomists as to how many genera and which ones should be recognized.

The position of the genus *Chaenomeles* within the Maloideae is not clear. The numerous seeds in each locule indicate that *Cydonia* and *Chaenomeles* are primitive in this respect, and *Pyrus* and *Malus*, with only two seeds in each locule, are more advanced. The characteristic of the number of seeds induced Decaisne (1847) and Wenzig (1874 to 1883), in accordance with most of the authors recognizing only the two genera *Cydonia* (including *Chaenomeles*) and *Pyrus* (including *Malus*), to consider *Chaenomeles* most closely related to the genus *Cydonia*. On the other hand the morphology of the flower (stamens and styles) and of the fruit, and the presence or absence of grit cells placed *Chaenomeles* closer to *Malus*, and *Cydonia* closer to *Pyrus*. Koehne (1890) suggested an evolutionary scheme of the Maloideae, in which the genera evolved from *Sorbus* in six distinct lines, and he is also followed by Dippel (1893).

Unfortunately, the results provided by anatomical investigations do not agree with the conclusions reached by observations on the gross morphology. The anatomical investigations are also contradictory, for so far only one characteristic has been considered at a time. If the size of the vessels and the number of cells in the width of the vascular rays are considered

alone (Burgerstein 1896a, 1896b, 1898a, 1898b), *Chaenomeles* is closer to *Pyrus*, and *Cydonia* to *Malus*. If the presence or absence of a tertiary thickening in the vessels (Burgerstein 1898a) or the anatomy of the leaf (Gérard, 1884) are the only characters chosen, *Chaenomeles* and *Cydonia* are more closely related, as are *Pyrus* and *Malus*. The divergence of conclusions reached by independent study of the gross morphology or of the anatomy has been pointed out by Burgerstein (1896a), and Folgner (1897).

The taxon *Cydonia sinensis* presents difficulties in the distinction of the four closely related genera *Chaenomeles*, *Cydonia*, *Pyrus* and *Malus* (*Docynia* not being well enough known). This species has been placed successively in the four genera mentioned, in *Malus* by Dumont de Courset (1811), in *Cydonia* by Thouin (1812), in *Pyrus* by Poiret (1816), and in *Chaenomeles* by Koehne (1890). Schneider (1906a) established a special section for *C. sinensis* which fitted so poorly in *Chaenomeles* that within the same year he (Schneider, 1906b) raised it in rank to form the monotypic genus *Pseudocydonia*. According to Burgerstein (1898b), *C. sinensis* is "eine Brücke" between *Cydonia oblonga* Miller and *Chaenomeles speciosa*.

The basis for the transfer of *Cydonia sinensis* to *Chaenomeles* by Koehne is not clear. He wrongly stated that the styles are fused. The only characteristics *Cydonia sinensis* shares with *Chaenomeles* are the glabrous fruits with deciduous sepals, serrate leaves, and an Asiatic origin (extinct in the wild), while it shares more than 35 other generic characters with *Cydonia*. Moreover, all the three species of *Chaenomeles* have fertile hybrids between them, while crosses of *Chaenomeles* species with *Cydonia sinensis* have been attempted several times but have always failed. The fact that *Cydonia oblonga* has entire leaves while *C. sinensis* and *Chaenomeles* have serrate leaves must not be given much weight, even if convenient in a key. The first few leaves of *Cydonia oblonga* seedlings are often serrate and later appear with entire margins. The fact that the calyx of *Cydonia sinensis* is deciduous, in contrast to the persistent calyces of *Cydonia oblonga*, is also unimportant for this character varies on individual shrubs of *Chaenomeles*. Rubsow (1944) noted that all the primitive species of *Pyrus* have a deciduous calyx, while the more advanced species have a persistent calyx.

Burgerstein (1896a, 1896b, 1898b) studied the wood structure of *Cydonia sinensis* and found it to correspond more closely with the structure of *Chaenomeles* wood than with that of *Cydonia* wood. From his wood study, this author considered *Cydonia* and *Chaenomeles* as distinct, and the latter as including *C. sinensis* (as suggested by Koehne). In 1898 he observed for the first time the flowers of *Cydonia sinensis* on a tree growing in the Vienna Botanic Garden. Burgerstein was forced to admit that the styles are free and not fused, as he had previously believed. This fact must have disturbed him, for in 1901 he published a paper, accompanied by a good colored plate, entirely devoted to this species, which he reassigned to *Cydonia*. His anatomical key to the genera of the Maloideae

did not correspond to the morphological affinities he observed in the styles, and he united *Cydonia* and *Chaenomeles* again. Burgerstein is the only botanist so far who arrived at this conclusion after having studied both genera.

Excluding Burgerstein's opinion of the validity of the genus *Chaenomeles*, all other taxonomists who have studied *Cydonia* and *Chaenomeles*, namely Bean (after 1951), Carrière, Decaisne, Koehne, Koidzumi, Nakai (after 1916), Rehder (after 1914), and Wenzig (after 1883) have concluded that they are distinct genera. This conclusion might have been reached more easily if the limits of the two genera were not somewhat blurred by the incorrect position in which Koehne placed *Cydonia sinensis*. There is a tendency often to delay a change of name in a nursery catalogue, sometimes even against horticultural knowledge. It is shown here in the reluctance of Goldring, Grignan, Hemsley, Mottet, Planchon, Späth, and Sweet to accept the conclusion that *Chaenomeles* and *Cydonia* are distinct; and some even persisted in placing *Chaenomeles* species in the genus *Pyrus*.

In spite of the reservations of some botanists and horticulturists, the recognition of the genus *Chaenomeles* is justified. The three species it includes, *C. japonica*, *C. speciosa*, and *C. cathayensis* form a good taxonomic unit, based on their geographic distribution, their morphology, and their breeding behavior. The three species do cross with each other but do not cross with species of other genera. Within the Maloideae, *Chaenomeles* possesses characteristics more primitive than the other genera, such as numerous seeds and numerous stamens in 2 rows, but it also shows a tendency toward unisexual flowers, which is to be considered an advanced character.

The genus *Chaenomeles* has not been found as a fossil in Japan (Tanai, 1961), in spite of the fact that several Rosaceae were recorded in the Tertiary flora of the island and that the leaves of Japanese Quinces should be easily recognized by their serrations. *Chaenomeles* is perhaps a relatively recent immigrant in Japan, having evolved in China in the Yunnan region, where two of its species are still found.

## MORPHOLOGY AND ANATOMY

The morphology of the genus *Chaenomeles* was studied on living specimens observed over a period of three years. These observations showed the unsuspected extent of variability existing in each individual and permitted consideration of the characters commonly used to distinguish the genus *Chaenomeles* from closely related genera, as well as those used to separate its species. A survey was also made of the anatomical characters of *Chaenomeles* to determine if any feature would distinguish this genus among the Maloideae.

**Roots.** The roots are numerous, fasciculate, and relatively superficial. In an old shrub, there may be several main roots, reaching up to 3 cm. in diameter.

André (1872) reports having observed in the Simon-Louis Nursery, Metz, France, roots which when dug up to make root cuttings, were bearing flower buds. One of these root fragments, left on a table, produced flowers which opened within a few days. André's figure shows flowers with long peduncles, but on an otherwise normal spring inflorescence. Twice, at the Arnold Arboretum, we observed flowers coming up through the ground, without being able to ascertain whether they were attached to a root or to a rhizome. The inflorescences were of a special type, and will be discussed further on.

**Habit.** There are three growth-forms in *Chaenomeles* corresponding to the three species. *C. japonica* has numerous spreading branches which completely cover the ground, and when in contact with it have a tendency to form adventitious roots. *C. speciosa* possesses many branches which are erect at first, and then spreading. Plants of this species increase by new suckers which, when left without control, may cover extensive areas. *C. cathayensis*, in contrast, possesses only a few straight, erect branches, with numerous short lateral branchlets terminated by a spur. These plants have a stiff appearance and can be trained as small trees.

The interspecific hybrids usually show an intermediate shape, but there are a few exceptions. *C.* × *superba* 'Crimson and Gold' tends to spread, forming a mat up to 50 cm. high on the ground, as would a pure *C. japonica*. Two cultivars of *C. speciosa*, 'Spitfire' and 'Starlight' have a characteristic vase shape due to numerous straight branches. Several cultivars show abnormal branching as indicated by their names 'Fastigiata', 'Pendula', 'Contorta', and 'Tortuosa'. In 'Contorta' the mutation affecting the shape of the branches (which change direction at each node) is carried into the progeny, or at least part of it, even though the other parent has normal branching.

The method of training Japanese Quinces along a wall, in common use in England, indicates how the shape of a shrubby plant may easily be changed, even with a minimum amount of pruning. The natural shape seems also to be modified through the influence of heavy snow cover. The hybrids of *C. cathayensis* often lose their branches completely, due to cold. The parts protected by the snow usually survive and start new shoots the following spring. On old plants, the snow may produce an artificial spreading form by repeated elimination of the straight, erect branches. In very cold winters, flower buds of *Chaenomeles* freeze above the snow line. The hardiness of *C. japonica* is probably due to its low habit rather than to intrinsic physiological qualities.

**Buds.** There are three kinds of buds, leaf buds and flower buds, both well formed, and adventitious buds.

The pointed and round *leaf buds*, usually 1 to 2 mm. long, are covered by a few pubescent, loosely imbricate scales. There are no true terminal buds since the long shoots are either terminated by a spine, or keep growing until the fall, when they are killed back by frost. The vernation is con-

duplicate, in contrast to the involute vernation of *Pyrus* and of some species of *Malus*. When the leaf buds are dissected, numerous brown imbricate scales, ciliate at base, or with tufts of trichomes at base and apex, and varying in size, may be seen. Within are about 4 to 8 embryonic leaves, with petioles already visible by the end of the summer and, in the center, meristem which will produce the next year's long shoot. The glabrous, embryonic leaves appear entire, but are bordered by narrow, ovate, transparent glands, lined side by side, and directed toward the tip. When the leaves unfold, the petioles grow faster than the blades, representing at one time ⅓ to ½ of the leaf, but in mature leaves only ⅕ to ⅛ of the length. Before the inner leaves have finished unfolding, the glands may be seen to secrete liquid.

The *flower buds* are formed early in the fall. The 1 to 6 flowers contained in each bud start to expand at the end of the summer, breaking up the bud. Ciliate scales surround the young flowers which spend the winter in a very advanced stage. By October, the flower color can often be recognized. In fact, the flowers are ready to open in a few days, at about any time from November, and often do, if the cold weather does not interrupt their development. This is why branches of Japanese Quinces are so easily forced for sale as cut flowers. In spite of this precocity of pigmentation of chlorophyll and anthocyanins, meiosis for most buds occurs in the spring.

The buds do not show specific differences in *Chaenomeles*. In order to identify the shrubs in winter condition, the shape of the branches, the spines, and the warting of the twigs normally present good characters for distinguishing the species. In cultivation, the abundance of interspecific hybrids showing intermediate characters renders this method very uncertain, however.

**Shoots and spines.** There are two main types of shoots in *Chaenomeles*, as in the closely related genera, which represent long and short shoots. These appear at different times of the year and spend the winter in distinctive stages, the long shoots as shoot "primordia," and the short shoots as "stemless" embryonic leaves.

The *short shoots* develop first, nearly simultaneously with the flowers, usually the first week of May in the climate of Boston. They appear on old branches as well as on the long shoots of the preceding year, without any indication of future development into long shoots. They bear four to eight fasciculate leaves varying widely in size, the outer ones being ⅒ to ½ the size of the inner ones. The outer leaves are frequently malformed, subentire (but with glands), and often emarginate or with a dry tip. They are usually promptly caducous. As the inner leaves unfold, the glands terminating the veins form the tip of each serration, alternating with a gland in each indentation.

On the long shoot of the preceding year, a spine axillary to the leaves with a bud on each side may often be observed. In *C. cathayensis*, one of these buds develops into a short shoot which may be located on the right,

or on the left of the spine, but it will be on the same side all along the branch. The buds on the other side of the spines will remain dormant under a large scale, for one or a few years, and may later produce flowers. In *C. japonica*, buds produced basally on both sides of the spines usually produce short shoots, giving a characteristic bushy appearance to this species. *C. speciosa* normally does not have spines axillary to each leaf of a long shoot, but rather has one bud produced at each node. The leaves of the short shoots are produced within a few days. The shoots terminate in a bud, which may or may not produce a spine.

After the leaves have expanded on short shoots, and by the middle of May in New England, a second flush of growth takes place. From this time on, *long shoots* only will be produced until the following spring. Leaves of long shoots do not differ in shape or size, but they are accompanied by large, paired reniform stipules, contrasting with the exstipulate leaves of the short shoots. New long shoots appear at the apex of last year's long shoots, if these have been interrupted and partially killed back by frost. The last living axillary bud, or many of the upper ones, may at once start to produce long shoots. New long shoots rarely appear if the long shoot of the preceding year was terminated by a spine. Long shoots located at the tip of branches do not usually ramify during the first season. The straight lateral branchlets occurring at right angles with the main branches, typical of *C. cathayensis* and its hybrid *C.* × *californica*, are formed on long shoots during the second season. Each axillary bud will produce a long shoot which is terminated by a strong spine or spur. Very often flowers will be borne on these short branchlets and in *C.* × *californica* long shoots will appear as a continuous mass of flowers along most of their length.

Long shoots, when expanding, are usually covered with a short and scabrous tomentum. The trichomes are unicellular, unbranched, and slightly bulbous at the base. They fall off the first summer without leaving a scar in *C. cathayensis* and in *C. speciosa*. In *C. japonica* where the trichomes are more abundant, the bulbous hair bases persist and appear as dark warts on the shoots during the second year. As the twigs enlarge in girth, the warted epidermis is shed during the second summer, and is replaced by a smooth bark. The presence of warts on the second year twigs is a characteristic of *C. japonica* and its hybrids. The old warted epidermis persists longer around the nodes, and can sometimes be found after the second year. Temporary warts occur exceptionally in *C. speciosa*, and have been observed in at least one herbarium specimen from China, where hybridization with *C. japonica* is very unlikely.

Spines may be formed very early, axillary to a leaf in a long shoot, especially in *C. cathayensis*. Most of the time, however, they appear only in the summer, terminating either a short shoot, or a long shoot. They are slender at first, straight, and probably increase in diameter during the second year. Young spines show by their occasional pubescence, or the presence of buds, that they are modified long shoots. The spines are stouter and more abundant in *C. cathayensis*, more slender in *C. japonica*,

and show an intermediate condition in *C. speciosa* and in the interspecific hybrids.

A few cultivars have been named for a lack of spines, however, there are usually a few on old shrubs of these spineless cultivars. *C. speciosa* 'Contorta', and *C.* × *superba* 'Tortuosa', in addition to unusual branch form, possess hooked spines, the points of which are directed toward the base of the branch. The curvature is evident as early as the spines appear from the buds.

Abnormal production of long shoots has been observed in the following cases: after the shrubs have been killed back to the ground or severely damaged by frost; after application of a weed-deterrent; and after an extremely severe attack of insects.

After a killing frost, long shoots are produced by adventitious buds at the base of the plant. These shoots are abnormally vigorous. They grow and ramify very rapidly, reaching as much as 1 meter in length within a few weeks. The pubescence is reduced or completely absent, the epidermis shedding off soon after being produced. Spines often appear immediately, axillary to each leaf, at least in *C. cathayensis*. The leaves and stipules of these shoots attain greater size than those in the crown of the shrubs.

Following the application of a weed-deterrent (Simozine), in September 1961, an abnormal production of long shoots was observed on many young plants of *Chaenomeles* in the Arnold Arboretum. The reaction seemed to be similar in the different cultivars which were affected. As an immediate response, long shoots were produced from adventitious buds located at the base of the shrubs, some reaching 80 centimeters or more three weeks after the application of the weed-deterrent. These shoots were often ramified, but could be distinguished at once from shoots produced after a frost effect by their abnormal leaves and stipules which were, in most cases, extremely narrow and showed discoloration. The leaves appeared variegated and colored pink by anthocyanin pigments. Green pigmentation, chlorophyll, was present in many only along the midribs. These abnormal shoots were especially sensitive to subsequent frosts.

In Cincinnati, Ohio, a very severe attack of seventeen-year locusts occurred in the summer of 1959. In the spring of 1962, *Chaenomeles* shrubs badly damaged three years before were observed at the Stanley M. Rowe Arboretum in different stages of recovery. In many branches the tips were affected so much that they had died back. In such cases, new long shoots were formed from the buds which otherwise would have produced short shoots. Since the branches attacked by the seventeen-year locusts have a tendency to crack open, the living part was often limited to one side. When this happened, all long shoots were produced on this same side, changing radically the ramification which normally alternates along the axis.

**Anatomy of the stem.** In a young long shoot, a large part of the stem is occupied by pith consisting of round cells containing starch grains. Each of the numerous vascular bundles, distinct at this stage, has a cap of

fibers. The rays are uniseriate. In the cortex, the cells of the ground tissue are loosely arranged and contain chloroplasts and starch grains. The epidermis is brown, as are the simple unicellular trichomes.

In a one-year old stem of *C. japonica*, the trichomes have been shed and a multicellular wart has developed replacing the bulbous base of the deciduous hair. The epidermal layers consist of about four rows of cells arranged tangentially to the axis.

Older stems show a star-shaped pith formed by loosely arranged round cells. The proportion of pith is much smaller in older stems than in young shoots. Diffused through the pith are patches of vertical parenchyma. The uniseriate or sometimes biseriate rays originate in the metaxylem. The annual rings of irregular size are well marked. The wood is diffuse porous but more vessels are formed in the spring. The vessels are usually solitary, or rarely two to three together. The diffuse vertical parenchyma is abundant among the fiber tracheids. The region of functioning secondary phloem is very narrow. The metaphloem consists of a few rows of crushed phloem elements. The protophloem appears as isolated patches of primary phloem fibers. The cortex is formed of 8 to 10 rows of cells tangentially arranged, with many intercellular spaces. Forming the periderm, are the phelloderm, the phellogen, and the phellem consisting of smaller rectangular thick-walled cells, tightly packed together. In *Pyrus*, according to Esau (1953), the periderm originates partly in the epidermis, and partly beneath it. The same is true of *Chaenomeles* in which the wood is very similar to that of *Pyrus*. The cells of the epidermis are light brown in color.

In radial and tangential sections the rays can be observed to be homogeneous, formed of round to oval cells, and non-storied. They can be from 25 to 45 cells high. The vessel elements show simple perforations. The walls are reinforced by spiral thickenings. Between the vessels and the fiber tracheids are alternate to opposite bordered pits. Simple pits are found between the ray cells.

The only specific difference observed in the stems is the difference in growth rate between *Chaenomeles japonica* on one hand, and *C. speciosa* and *C. cathayensis* on the other. For a given stem diameter, *C. japonica* may show twice as many growth rings as the others. *C. japonica* is the only species to show warts on the epidermis of the one-year shoot. The first epidermis is shed during the second year, and after that the stems of *C. japonica* appear as smooth as those of the other species.

**Node and petiole.** In a long shoot of *Chaenomeles*, the node shows three traces coming from three gaps. In the pulvinus, the two lateral traces divide, one branch of each going into the stipule, the other into the petiole. The three traces inside the petiole fuse together and form one trace along the length of the petiole. According to Howard (1962), this pattern represents three traces from three gaps, with bundles fusing to form a simple arc by simple marginal fusion of the traces. In the pulvinus the petiole has the shape of a half circle. Under the epidermis are one to

two rows of large brown cells, tangentially arranged. The rest is occupied by parenchyma and by the vascular bundle appearing as a smaller half circle in the center with xylem on the adaxial side and phloem on the abaxial side. At the base of the petiole there are no fibers. By the middle of its length, fibers occur in patches forming a broken arc outside of the phloem. Higher up the petiole changes shape as small wings are formed at the adaxial corners. A patch of fibers is found in each wing. In the upper part of the petiole, the traces appear which form the pinnately arranged veins. The first two veins do not leave the midrib at exactly the same point. One appears first, then the other, followed rapidly by the third and the fourth veins on alternating sides.

Unicellular trichomes are occasionally found on petioles, and are a regular feature on the midribs of *C. speciosa* and on the abaxial surface of *C. cathayensis*. In contrast to *Cydonia*, there are no glands on the petioles of *Chaenomeles*.

**Leaves and stipules.** In *Chaenomeles*, the leaves offer excellent characteristics for distinguishing species (FIG. 4). *C. japonica* possesses obovate to spathulate leaves often terminated by an indentation, and coarsely crenate on the margins. In contrast, the leaves of the other two species are serrate. In *C. cathayensis*, the leaves are elliptic to lanceolate, finely and sharply serrate, each serration terminating in an awn-like tip. *C. speciosa* has ovate to oblong, sharply serrate leaves. The type and amount of pubescence is a characteristic of the species, and is as useful as the serration for recognizing the parents of a hybrid. In *C. japonica*, the leaves are usually completely glabrous, even when unfolding, and only rarely have a few short hairs on the midrib of the under surface. *C. speciosa* is usually pubescent on the midrib of the under surface (exceptionally so on the upper one). *C. cathayensis* has leaves often completely covered, when young, by a fulvous tomentum underneath but when the leaves expand, the tomentum may become thinner or fall off. *C. cathayensis* var. *wilsonii* (Rehd.) Bean, was based on the presence of this tomentum, which in reality occurs in variable abundance in individual adult plants.

In transverse section the leaf shows a normal bifacial structure. Under the epidermis of the adaxial side, are two to three rows of palisade cells above the spongy parenchyma. The vascular bundles are surrounded by a bundle sheath consisting of parenchyma cells. Stomata are restricted to the lower epidermis. The guard cells are reniform.

The leaves of *Chaenomeles* are serrate, each serration and alternating indentation ending with a gland. In cross section it can be seen that both phloem and xylem elements terminate just below the tip of the gland. These tracheids are enclosed by bundle-sheath cells. The epithem, a thin-walled parenchyma without chloroplasts, is little differentiated from the spongy tissue. Glands are known to differentiate relatively early in leaf ontogeny and to function for a short time. In *Chaenomeles* they are nearly full size in unrolling leaf-buds. When functioning, the glands are transparent or tinted red by anthocyanins. The secretion can often be observed

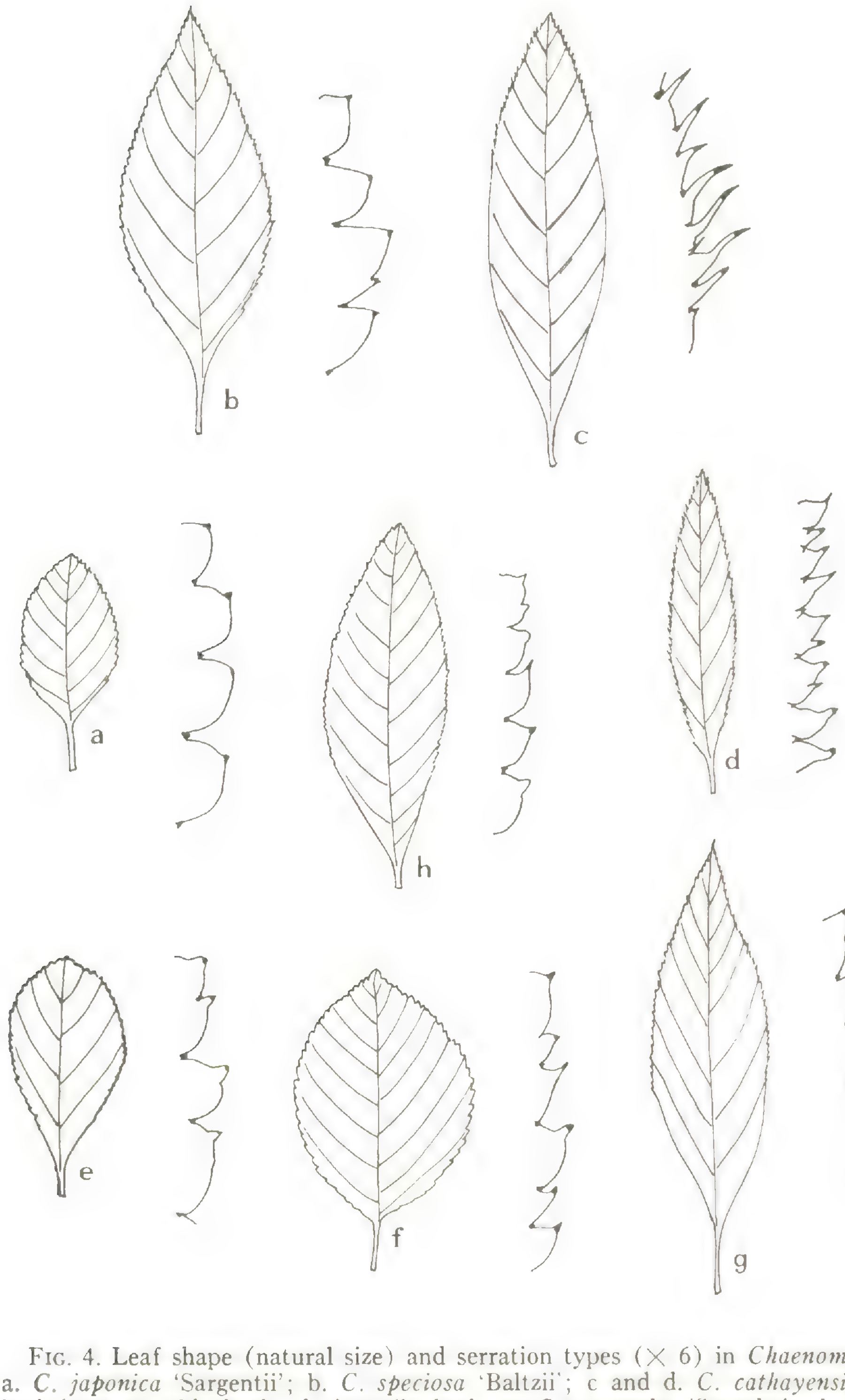


FIG. 4. Leaf shape (natural size) and serration types (× 6) in *Chaenomeles*. a. *C. japonica* 'Sargentii'; b. *C. speciosa* 'Baltzii'; c and d. *C. cathayensis*, c. leaf from an old shrub, d. juvenile leaf; e. *C* × *superba* 'Superba'; f. *C.*× *clarkiana* 'Minerva'; g. *C.* × *vilmoriniana* 'Afterglow'; h. *C.* × *californica* 'Rosemary'.

as dried transparent droplets on herbarium specimens. The foliar nectaries in *Chaenomeles* may be considered intermediate between hydathodes and glands by their position, their structure, and their relatively fluid secretion. As soon as the leaves mature and become coriaceous, the glands cease functioning and dry up according to Ono (1907). They appear dark-red or black on adult leaves.

Leaves on short and long shoots were compared in order to find if there were any morphological differences. The leaves have the same shape, type of serration, abundance of glands, and petiole length. Short shoot leaves may be larger than long shoot leaves appearing on the crown, but long shoot leaves of adventitious shoots or sprouts are the largest of all. The leaf size is so variable that it may vary ten-fold in one short shoot. Size and shape could not be used to distinguish isolated leaves as to origin on either long or short shoots. The only difference is the presence on leaves of long shoots of large paired stipules, and their absence on the leaves of short shoots.

The stipules are free, reniform, and show the type of serration and pubescence characteristic of the species. They vary in direct relation to the leaves, tending to be very sharply serrate when accompanying juvenile sharply serrate leaves, or nearly entire in some old shrubs of *C. cathayensis*. Occasionally, stipules have been found to be slightly lobed in three cultivars of *C. speciosa,* 'Alba Cincta', 'Shirataum', and 'Versicolor'.

In *Chaenomeles* the stipules are foliaceous and have palmate venation. A branch of the lateral trace of the petiole goes into each stipule. This divides rapidly into three or five bundles of uniform size. The epidermis is not as resistant as in the leaves and tears off easily. The reniform stipules have a bifacial structure with two rows of palisade cells on the adaxial side. The minor vascular bundles forming a reticulate pattern are located between the palisade cells and the spongy parenchyma, close to the abaxial surface. The bundle sheath consists of parenchyma cells, but only three or five veins possess a bundle sheath extension. The glands, stomata and trichomes are comparable to those of the leaves.

Critchfield's theory (1960) on leaf dimorphism in *Populus* finds application in *Chaenomeles* where dimorphism is expressed in the absence or presence of stipules. Critchfield found in *Populus* that a first type called "early leaves" laid down in the leaf buds in the fall and existing during the winter as embryonic leaves will be produced on short shoots and possibly at the base of long ones. The second type which spent the winter as leaf primordia will appear on adventitious shoots and upper parts of long shoots of the crown. He observed three types of shoots, one with only early leaves, corresponding to short shoots; the second with early and late leaves corresponding to long shoots; and a third type with only late leaves, found in adventitious shoots.

The same situation is encountered in Japanese Quinces. If there is an interruption between the development of short shoots and the start of the long shoots, the number of leaves (4 to 8) observed as embryonic in the bud will all be found fasciculate at the same level, and without stipules.

The production of stipules will start abruptly with the first alternate leaves of the young long shoot. When the long shoot develops without interruption, the first leaves, exstipulate, are alternate along the shoot. It is only when the supply of leaves (maximum 8) which spent the winter as embryonic leaves in the buds has been exhausted, that the leaves with stipules start to be produced. The production of all exstipulate leaves in a fascicle, or their successive production along an axis, is certainly dependent on the weather.

It is not known why stipules are produced only in long shoots, but this may be observed in *Pyrus*, *Malus*, and *Cydonia* which have less showy stipules than *Chaenomeles*, and also in *Platanus*, a member of the same order, the Rosales. Stipules are also always present in long shoots developing from adventitious buds, and in seedlings.

In *C. cathayensis* the juvenile leaves differ markedly from the leaves produced on adult shrubs. The juvenile leaves and their stipules are smaller, more sharply serrate, always glabrous, and so narrow as to look nearly linear. Their length can be as much as seven times greater than their width, compared to three to four times in the leaves of adult shrubs. It is not known how many years juvenile leaves persist in a plant which originated from seed. A shrub of *C. cathayensis* which germinated in 1936 at the Arnold Arboretum, and has been repeatedly killed back by frost every year, is still producing juvenile leaves on the sprouts it sends up each spring. In contrast, mature leaves can be obtained by grafting a scion of an old plant on a young understock. In *C. cathayensis*, mature or senile leaves often appear subentire and show a thick tomentum on the under surface.

The juvenile leaves of *C. japonica* and *C. speciosa* do not differ markedly in shape from their mature leaves, but are only slightly smaller. In *C. japonica*, the teeth of the crenate leaves are evident at a later stage than the fine serrations of the other two species. It is probably a case of allometric growth, since crenate and serrate leaves look alike during the embryonic stage in a bud or in a young seedling.

The foliage, as recorded in the last three years, appears during the last week of April, or more often the first week of May, in the climate of Boston. The first flush of growth during the blooming period produces fasciculate leaves on short shoots. These are nearly always green. By the middle of May to the middle of June the long shoots elongate. Their leaves are very often brightly colored pink or brown from an abundance of anthocyanin pigments. The coloration extends from the midrib toward the extremities of the veins, and the chlorophyll appears as green patches isolated in the reticulate red pattern. One cultivar at least, *C.* × *superba* 'Foliis Rubris' has been named for its red leaves. In spite of its name, the foliage coloration does not last any longer than in other cultivars. The cultivar which probably retains the red pigmentation longest is *C. speciosa* 'Kermesina Semiplena'. By the middle of July the foliage of all the Japanese Quinces appears glossy green and remains so for the rest of the season, except at the growing tips of the shoots.

Leaves of *C. japonica* and *C.* × *superba* are often a yellow-green, while *C. speciosa*, *C. cathayensis* and the other hybrid groups usually possess leaves dark green on the upper surface and lighter below. Two cultivars have been named for their variegated foliage, *C. speciosa* 'Foliis Variegatis' and *C. japonica* 'Tricolor'. *Chaenomeles japonica* 'Tricolor' which is still in cultivation shows leaves of three colors, pink, green, and white, on the new long shoots. Mature leaves are green or variegated green-and-white. An albino mutation was observed by Simirenko (1888) on a branch of *C. speciosa* in which all the leaves were white, without chlorophyll. Simirenko named it 'Simirenkiana' and grafted it on normal understock in order to produce Japanese Quinces with white leaves. On this branch the flowers were also of a lighter shade than on the rest of the shrub. The fate of this "cultivar" is unknown.

In areas with dry hot summers Japanese Quinces may lose some of their leaves in midsummer. Some nurserymen suggest that by removing the fruits, or growing cultivars with weak fruit production, defoliation will be prevented. This fact is contested by other horticulturists, and has not been proved one way or another. Chlorosis has been observed on *Chaenomeles* growing in lime soils.

In the autumn the leaves fall gradually, being mostly gone by November 10. There is no fall coloration of any kind, unlike most species of *Cydonia*, *Pyrus*, and *Malus* which color brightly in red, or at least tint with yellow, before falling. In warmer climates *Chaenomeles* is reported to have nearly persistent leaves.

As observed, the leaves, especially when young, are less resistant to cold than the flowers. With a late frost in the spring leaves can be damaged, appearing crinkled when unfolding, although the flowers are not touched.

**Inflorescences.** Along with the tendency to flower at any time of the year, weather permitting, *Chaenomeles* presents a great variety of inflorescence types. A few cultivars have been named for their long peduncles, such as *C. speciosa* 'Pedunculata'. These pedunculate inflorescences appear on any shrub if heat, light, and humidity are sufficient. They are not a varietal character, but rather a seasonal phase.

In *Chaenomeles*, the inflorescences vary from one to six subsessile flowers appearing together at one point, to a very elaborate raceme or panicle, sometimes including leaves, stipules, and bracts. A correlation with the short and long shoots may explain what kinds of responses are brought about by the environmental conditions. The different inflorescences, modifications of cluster, spike, raceme or panicle, which can be found on any one shrub are of two main types, one being analogous to a short shoot, the other to a long shoot. An intermediate type is sometimes observed.

The *short shoot* type is found in the spring and in the late fall (FIG. 5 a; FIG. 6 a, 6 e). Its flowers have spent months in an advanced embryonic state in an open bud. They are clustered, (1) 2 to 6, on old wood or on the long shoots of the preceding year. The flowers have extremely short

FIG. 5. Inflorescence types (natural size). a. Spring inflorescence, with short pedicels, of *C.* × *californica* 'Arthur Colby' (May 4); b. fall inflorescence of *C. speciosa* 'Phylis Moore' (October 2); c. summer inflorescence of *C. speciosa* 'Phylis Moore' (May 28).

or non-existent peduncles, and no bracts. This is the normal type of inflorescence at blooming time in early spring, before the leaves appear. If branches are lying on the ground partially buried in mulch, the flower buds will develop in the same manner, but the peduncles will expand in order to reach the surface. In any case, each flower peduncle will be distinct from the others.

Flower buds are formed very early. If the cold weather does not set in, flowers which were prepared for the following spring start to open in late fall. It is difficult to tell whether the inflorescence type consisting of a few sessile flowers, fasciculate at one node, is brought about by a return of the early spring conditions of temperature, humidity, short days, and absence of leaves, or whether it depends, as in short leafy shoots, on the advanced embryonic condition of the flowers in the buds.

An intermediate situation between short and long shoots has been observed several times in living plants as well as on herbarium specimens. The bud produces a short shoot during the spring like any other short shoot. It is continued, sometimes without interruption of growth, by a slightly branched cluster of three to five pedunculate flowers. No leaves, stipules or bracts are produced and the whole inflorescence is not more than two to five centimeters long. Normally, a short shoot does not elongate and forms a bud at the end, often destined to produce flowers the next spring. For an unknown reason these flowers develop the same season. This intermediate condition may be found in late spring and in early fall (FIG. 6 b).

The *long shoot* type of inflorescence occurs from late spring to late fall. So far, it has not been possible to predict where and when summer inflorescences are going to appear. At this time, the shrubs are covered with leaves. Summer inflorescences, like sprouts, develop very fast if the temperature is favorable. When they can be recognized, it is too late to find out in what kind of embryonic condition they spent the winter. This can be deduced by their location, often on old wood, even on the main branches, and also by the fact that at this time of the year there are only rudimentary dormant buds. Summer inflorescences, like the long leafy shoots, probably spend the winter in a primordial stage.

The peduncle length appears to be dependent on the temperature, a few degrees change at night probably being enough for change from a spike to a raceme or a panicle. The variation in long shoot type of inflorescence is even more striking, involving the presence or absence of leaves, stipules, bracts, or intermediate organs, as well as the transformation of the sepals into leaves. This type of inflorescence is extremely variable and may be subdivided into four categories.

1. A few exstipulate leaves are found at the base or along the axis. They are succeeded by leaves with small stipules. Axillary to each leaf is a flower or a ramified branchlet with two or more flowers associated with bracts. The shoot is terminated by a flower. Unbranched, it may be a spike or a raceme, when branched, a panicle. It may reach a length of 20 centimeters in a few days. This is the commonest inflorescence type in the summer and occurs from late spring to fall (FIG. 5 c).

2. In a variant of the preceding the leaves, usually not more than six, lack stipules. The flowers may occur in the axils of the leaves or above them. Bracts are usually absent. This type is common in the fall. The inflorescence may reach 20 centimeters or more (FIG. 5 b).

3. A third and infrequent type of inflorescence may be formed in the fall. A

FIG. 6. Inflorescence types (natural size). a. Spring inflorescence, with long pedicels, of *C.* × *superba* 'Perfecta' (May 10); b. intermediate inflorescence of *C. speciosa* 'Simonii' (June 25); c. fall inflorescence, with heart-shaped bracts and foliaceous sepals, of *C. japonica* 'Sargentii' (November 10); d. inflorescence appearing through the ground, of *C. japonica* 'Sargentii' (June 6); e. late fall solitary flower of *C. speciosa* 'Simonii' (November 17).

few exstipulate leaves are laid down at the base. The whole shoot ramifies and heart-shaped, serrate organs, intermediate between leaf and stipule, are found in place of the usual inconspicuous bracts. This modification is carried out to the

calyx which becomes foliaceous. These leafy bracts and sepals bear glands on each tooth. It is not known if they ever secrete any liquid (FIG. 6 c).

4. In two instances, in summer and early fall, inflorescences were found coming up through the ground. One was formed on a very old shrub of *C. japonica* 'Sargentii', and the other, on a young plant of *C.* × *superba* 'Elly Mossel'. The shoots elongated through the ground, without bearing any leaves. Once in the open they developed bracts, some normal, others heart-shaped, then flowers with foliaceous glandular sepals (FIG. 6 d).

Sometimes there are other abnormalities accompanying foliaceous bracts and sepals such as glands appearing away from the edges (on the adaxial side only, and always connected with veins), stamens transformed into petals or sterile styles with extra branches, and so forth.

At least some of these different types of inflorescences are common and usually appear at the same season year after year, probably as a response to similar environmental conditions. They cannot be associated with any particular species or cultivar. On one shrub of *C. japonica* 'Sargentii' which originated from seeds brought back by Sargent from the mountains of Japan, six of the seven types and subtypes have been observed during the last two years. Summer inflorescences are so frequent that not only cultivars, but also botanical species or varieties have been named for these seasonal phases. The type of *C. speciosa* (Sweet) Nakai, an illustration, plate 692 in the Botanical Magazine, represents an inflorescence intermediate between a short and a long shoot. The syntypes of *C. japonica* var. *pygmaea* Maximowicz are specimens, collected in flowering condition in December, of the short shoot type with long peduncles, appearing exceptionally in late fall. Other characteristics which vary according to the temperature were included in the original description.

The different types of inflorescences found in *Chaenomeles* at different times of the year encompass the range of inflorescences found in the closely related genera. Since these genera have a limited blooming period, only one type of inflorescence occurs which is considered characteristic of the genus. *Docynia* possesses a few clustered subsessile flowers. They are analogous to the spring inflorescences of *Chaenomeles*, and comparable to those of short shoots. *Malus* has the short shoot type of inflorescence with long peduncles. *Pyrus*, also some species of *Malus*, present the intermediate situation with fasciculate leaves and a slightly branched, but short and naked inflorescence in the center. This has been called "pyrostele" by Bailey (1949a) who thought that this type was peculiar to *Pyrus*. This term is unfortunate for the confusion it can cause with the anatomical meaning given to the term stele. *Cydonia* possesses solitary flowers occurring at the tips of leafy shoots. This inflorescence is a typical modification of a long shoot, which in *Chaenomeles* ends up with a spine, or is modified into a branched inflorescence. The different types found in these four genera develop at the same time as the corresponding types in *Chaenomeles*. Consequently, they must not be considered as genetically determined, but rather as arising in physiological response to the environment.

**Flowers.** The variation in inflorescences found on any one shrub is matched by an equal or greater variation found in the flowers. Normally, flowers are produced from special buds, early in the fall. In the spring, flowers open within a few days in good weather. They usually open before the leaves, but the leaves develop and start to unfold when the petals are still present. The aestivation of the sepals and petals is imbricate, as in *Pyrus* and *Malus*, and in contrast to the contorted condition in *Cydonia*.

The hypanthium forming the base of the flower varies from cup-shaped to gourd-shaped. There is a tendency for the hypanthium of *C. japonica* to be more nearly cup-shaped; for *C. speciosa*, more gourd-shaped; and for *C. cathayensis*, to have an elongated hypanthium. Moreover, the shape of the hypanthium is complicated by the presence of numerous unisexual flowers in every species, which are more nearly cup-shaped when entirely male, more nearly gourd-shaped if entirely female. This does not always hold true, for flowers with long hypanthia sometimes have no ovules, and flowers with short hypanthia may have ovules which appear superficially to be borne in the peduncle. The receptacle, formed of the hypanthium and prolonged by the 5 sepals is always glabrous. It is woolly or at least pubescent in *Cydonia*, *Docynia*, and *Pyrus*. In *Chaenomeles* the receptacle is often brightly colored purple or brown on the sunny side, by anthocyanin pigments.

The sepals appear as five short truncate or round, ciliate lobes, without glands, but pubescent inside at the place where the petals are attached. The lobes, often unequal in size, are always erect at anthesis. In contrast, the sepals are reflexed in *Cydonia* and *Pyrus*, and are glandular in *Cydonia* and *Docynia*. The calyx lobes, as well as the hypanthium of which they are a prolongation, are very much vascularized by anastomosing traces. The sepals are ciliate with single unicellular trichomes.

Sepals can show two abnormalities. They may either become leaf-like, a relatively frequent condition, or more rarely, petal-like. Foliaceous sepals occur normally on at least two types of inflorescences, and in this case, they are serrate and glabrous on the edge, each serration being terminated by a gland. They are pubescent inside, as usual. If only partially leafy, the entire edge will be ciliate, and the trichomes are abruptly replaced by glands where the serrations begin. A partial development of petal-like sepals is sometimes found. This latter case is of common occurrence in *C.* × *superba* 'Texas Scarlet'.

The genus *Chaenomeles* normally has five regular, free, slightly unguiculate round petals. They are borne on the hypanthium, opposite the sepals. They may be carinate, especially in *C. japonica* and *C.* × *superba*, undulate, or flat at the end of anthesis. The petals are short pubescent on the claw, glabrous otherwise, and have exceptionally been found to be ciliate and bordered with small capitate glands in *C.* × *superba* 'Crimson and Gold'. The petals possess slightly larger cells than the sepals, and are less vascularized. At least three traces enter each petal. They divide dichotomously and the veins anastomose to form a reticulate pattern often reaching the edge of the petal.

Petals are never less than five, but when broad and overlapping the flowers appear semidouble, even with a regular number. Often, there are more petals from a partial modification of stamens and the number may reach 15 which are quite variable in size and shape. Numerous cultivars with semi-double or double flowers have been named. This character may vary widely, flowers being double on a young shrub, or when the number of flower buds has been reduced by frost, single when the shrub is older and loaded with flowers. Isolated summer flowers often have a greater number of petals than spring flowers.

The genera *Cydonia* and *Chaenomeles* are cited as having petals which drop before wilting. They do so after four or six days, even before the outer stamens have shed their pollen, if the weather is hot. A longitudinal section of the flower reveals an abscission layer formed between the hypanthium and the petals. On both sides of this constriction the cells are smaller and more tightly packed. The abscission of the petals which are shed when perfectly turgid occurs at this constriction. The separation seems to start from the center and proceed toward the outside. Since stamens do not possess an abscission layer, petals on double flowers are not shed, and can often be seen to persist on young fruits. The double flowers last considerably longer than the single ones.

The petals of *Chaenomeles* cultivars can show a great array of colors, from white to darkest red, through all shades of pink, orange, and scarlet. Bicolored petals are also frequent. The color intensity and petal size are in direct relation to light, and probably to heat. In rainy spring seasons, flowers appear pale and dull. This relationship is also obvious from an observation of the flowers borne on one shrub from early spring to late fall. The color becomes more intense until August and September, reverting later to lighter shades. Very few cultivars are pure white during the summer months. The effect of light may also be observed by comparison of flowers opening at the same time on the outside and inside of a leafy shrub, or on double flowers in which the parts where the petals overlap remain uncolored.

Most cultivars have been selected and named on the basis of petal color. A classification of cultivars according to their color can only be approximate, due to the changes in intensity throughout the year. In addition to the weather, the soil may have an influence. Nakai (1916) is the only botanist who attempted to distinguish species by the color of the flowers alone. He raised *C. speciosa* var. *eburnea* to the rank of species and placed in it all the cultivated varieties with white petals.

As a reverse case from petaloid sepals, sepaloid petals may also be found. *C. speciosa* 'Simonii', with semidouble flowers, has outer petals often marked with a green line, the red colored parts appearing as two wings. The sepals of this cultivar are normal.

The stamens, 40 to 60 in number, are borne on the hypanthium below the petals, more or less in two rows. They are free and shorter than the petals. The filaments are glabrous, white or pink or dark rosy-red when developing in summer conditions. The anthers are introrse, basifixed at

first, becoming slightly versatile when old. They are yellow, turning to brown after the pollen has been shed. The extra petals in semidouble and double flowers are modified stamens which may retain one or more anther sacs on the edge. All transitional stages between stamen and petal can be found.

There is no constriction at the base of the stamens, rather a slight enlargement. The tissue of the hypanthium with its large cells arranged vertically continues without interruption into the filament up to the anther. There is one trace only entering the filament. The few protoxylem elements which form the vascular bundle show reinforcement by spiral thickenings. The center of the vascular bundle is often hollow. The vascular bundle stops at the base of the anther sacs, but diffused protoxylem elements may be found in the connective. The epidermis of the filaments, formed of very small cells, is cutinized. Stomata have been observed, but there are no trichomes present. Under the epidermis is another row of slightly larger cells around the ground tissue.

The anthers, in an early stage, show two lobes and four locules. Close to maturity the anthers have two locules only, by loss of the partition within each anther half. Beneath the epidermis is the endothecium which consists of large cells, tangentially arranged, their walls, except the one in contact with the epidermis, being reinforced by conspicuous secondary wall thickening strips oriented perpendicularly to the epidermal layer. There is an interruption of the epidermis and of the endothecium at the place where dehiscence will occur. The stomium is a longitudinal slit located between the locules of each half of the anthers. Before opening it is plugged by a chain of very small thin-walled cells. Just before dehiscence starts, the parietal layers inside the endothecium and the tapetum disintegrate and appear as collapsed or crushed cells.

In the double flowers, some of the stamens are petaloid. In longitudinal section, it may be seen that in spite of their change of function and color, they have a single vascular trace, and lack trichomes completely at the base. This sole trace divides much higher up in the claw and eventually produces a normal reticulate vein pattern. A fragment of anther is often retained, with or without pollen production. There is neither constriction at the base, nor small cells arranged tangentially to interrupt the tissue of the hypanthium. This explains why "petals" of double flowers do not shed as in single flowers. The outer or normal petals of double flowers do possess a constriction and are shed unnoticed, while petaloid stamens persist until the abscission of the top of the hypanthium occurs a few weeks after pollination.

Functionally female flowers are formed by the abortion of stamens and are less common than functionally male flowers. Although they are not recorded in the horticultural literature of *Chaenomeles*, functionally female flowers occur occasionally in many shrubs, or very frequently in such cultivars as *C.* × *superba* 'Alba Semiplena', 'Columbia', 'Early Apple Blossom', and 'Sunset'. Two shrubs of 'Columbia', grown side by side, have been observed for a few years to produce female flowers only. In the

spring of 1963, they both produced a few male flowers and no female ones. In these female flowers, stamens in reduced number were present but did not contain any pollen and often the anther sacs were transformed into pink appendages in the shape of horns.

The pollen grains of *Chaenomeles* are tricolpate, without ornamentation; the three germ pores are evident at the rounded corners. The exine between the pores is thick and smooth. In herbarium specimens of wild and cultivated plants, the pollen grains measure from 25 to 55 micra. There is a great variation in size of pollen grains coming from the same anther. The three species and their hybrids have been found to have pollen grains with the same range in size. The greatest variation in pollen size has been observed in a specimen of *C. japonica* collected in Japan. The grains measured from 15 to 32 micra. The pollen of the cultivars representing the interspecific hybrid groups has been found to be on the lowest part of the range, while the pollen of *C.* × *californica* 'Clarke's Giant Red', a tetraploid, was in the upper part of the same range. These measurements do not seem to be significant since the variation is so great in the pollen contained in one anther, and is no larger in cultivated plants or in hybrids than in wild plants. It is impossible to recognize the species or the genus by the pollen. The two species of *Cydonia* have similar pollen, also within the size range of *Chaenomeles*.

The proportion of bad or empty pollen grains which do not stain with aceto-carmine can be from $\frac{1}{10}$ to $\frac{1}{4}$ of the total. The proportion of empty pollen has not been found to be significantly different in hybrids and in species, or in cultivated specimens and in wild specimens. It varies a great deal on the same shrub at different dates, and seems to be dependent on weather conditions.

Between the inner row of stamens and the column formed by the fused styles, is a glabrous, nectariferous interval called a disc. The disc is larger in male flowers when the column formed by the styles is reduced in size or absent, than in predominantly female flowers. The disc covers the part of the carpels fused to the hypanthium and is the place where nectar is excreted. The epidermis of the nectary appears no different from that of the rest of the hypanthium. Beneath the epidermis, a nectariferous zone is several cells thick and extends in the form of a network. It consists of very small round cells, closely packed and staining differently from the ground tissue. When the cell content persists, it shows numerous small refringent granules. The floral nectaries differ anatomically from the leaf glands in lacking vascular bundles.

The column formed by the styles is characteristic of *Chaenomeles*, although it may vary widely within one species. The styles may be completely fused, in which case the column is solid, or partially fused, forming a hollow column. At the base are some straight unicellular trichomes which may vary from abundant to entirely absent. Trichomes are occasionally found within the hollow columns. Each style is vascularized by two to four traces. The ground tissue consists of large cells longitudinally arranged, and bordered by an epidermis. The styles are always free above.

The decurrent stigmata have a glandular papillate epidermis. The stigmatoid tissue of large and longitudinally arranged cells forms anastomosing strands connecting the stigmata to the ovules. These cells stain in the same way as the nectariferous cells, and also possess refringent granules. In longitudinal sections, the stigmatoid tissue may be observed very close to the reticulum formed by the nectariferous tissue. The two kinds of cells may be distinguished by their size.

The five styles in *Chaenomeles* are fused for ⅓ to ⅔ of their length. This is a generic character not present in the related genera which have free styles coalescent by the hairy covering. The column is commonly glabrous or glabrescent, less often pubescent, rarely woolly. It is always glabrous in *C. japonica*, pubescent to woolly in *C. cathayensis*, and varies from glabrous to woolly in *C. speciosa*, with the greatest number of cultivars being glabrous or glabrescent. Japanese authors put much emphasis on this character and still recognize Nakai's (1916, 1918, 1923, 1929) four "species," separated according to the pubescence of the stylar column: *C. eburnea*, glabrous; *C. speciosa*, glabrescent; *C. trichogyna*, villose; *C. extus-coccinea*, woolly. Nakai himself (1929), gave as synonym of *C. extus-coccinea* with a woolly column, the cultivar 'Alba Cincta' (as *C. japonica* var. fl. *roseo*, *albo-cincta*) which has a glabrous column. Such variation in the pubescence of the column is not correlated with other morphological characters. The part where the styles are free is always glabrous. The styles are white, exceptionally red (observed in summer flowers only). They terminate in green decurrent stigmata, comparable to those of *Cydonia* and *Docynia*, but contrasting with the discoid stigmata of *Pyrus* and *Malus*.

Many aberrations may take place in the styles. Often more than five styles, and up to nine, have been observed in the same flower. They usually correspond in number to the carpels, but extra styles may also occur by branching just under the stigmata. These extra branches are often found in flowers appearing in the fall. In some cultivated shrubs of *C. speciosa*, the styles are abnormal year after year. In a few flowers, they are fused into a hairy cone protruding above the petals. These flowers appear to have a superior ovary, in contrast to the normal inferior ovary of the Maloideae.

In other and common instances styles may vary from normal size, about ¼ longer than the stamens, to being completely absent. Every transition has been observed in the flowers of a single shrub, which can produce normal hermaphrodite flowers with long styles, others with styles of the same length as the stamens, some shorter, as well as flowers which are completely male by abortion of the female organs. Flowers are found with ovules and no styles or with normal styles and stigmata, and no ovules. In contrast to functionally female flowers which always contain sterile stamens, male flowers usually do not have styles or ovules. Contorted styles of normal size, but without stigmatic surface are extremely rare. Male flowers are very common, even in wild specimens. The syntypes of *Chaenomeles japonica* var. *pygmaea* Maxim. show male flowers only. So

does plate 692 of the Botanical Magazine which is the type of *C. speciosa* (Sweet) Nakai.

Under the disc are found the five carpels. They are completely fused to the hypanthium on the abaxial side, and fused together on the adaxial side. They form an inferior syncarpous ovary with five locules, but numbers from three to seven have been observed. Carrière (1876b) found a fruit in which the five carpels gave rise to ten locules by the production of false partitions perpendicular to the normal ones. Exceptionally, carpels are incompletely fused in the center (as in *Cydonia* and *Docynia*).

A transverse section through the ovarian region shows a cutinized epidermis formed by small cells without trichomes. Directly beneath the epidermis are two to three radially oriented rows of collenchymatous tissue of larger tightly packed cells. The ground tissue forming the bulk of the hypanthium and of the carpels, consists of large cells loosely arranged. Immediately internal to the collenchymatous tissue are numerous small vascular bundles forming an irregular circle. Near the inner side of the hypanthium are ten vascular bundles which vascularize the sepals and the petals. At the tip of each of the five carpels is another vascular bundle. Between the two circles is the boundary of the ovary and the hypanthium. These two organs are completely fused in *Chaenomeles* and are anatomically indistinguishable. The ground tissue of each is a loose parenchyma. At the time of anthesis there are no sclereids in either of them. However, only the ovary tissue has the strands of stigmatoid tissue. Each locule contains about 20 anatropous ovules with two integuments, arranged horizontally in two rows.

**Fruits.** The fruits of *Chaenomeles* are pomes as in the other Maloideae. There are two conflicting theories as to the interpretation of the inferior ovary in the Maloideae. The usually adopted one is the Axial Theory of the nature of the inferior ovary, also called the Receptacular Theory. In this theory, the hypanthium is considered basically axial, consisting, according to Eames (1961) of the rim of the receptacle. Under the Appendicular Theory, however, the hypanthium is considered to consist of the adnate bases of sepals, petals and stamens. Most authors commonly cite the Maloideae as showing inferior ovaries in which the receptacle has a prominent part. Eames, through comparative studies of the floral anatomy of the Rosaceae, and comparisons of proliferated rose and apple fruits, arrives at the opposite conclusion. For Eames, the fleshy outer part of the apple and the pear consists morphologically of the fused bases of appendages. The fruits of *Chaenomeles* in which the calyx lobes often persist and become accrescent, forming the upper part of the fruits, seem to accord with the Appendicular Theory.

The transformation of the ovary and the hypanthium into a pome occurs in the same manner as in the apple, which has been studied by several authors. The ripe fruit is brightly colored yellow by chromoplasts. The cuticle on the outer side has thickened; it may become sticky in some cultivars. The stomata have been transformed into lenticels consist-

ing of patches of suberized cells. In some fruits, patches of suberized cells occur also at random on the skin, especially near the apex. This corresponds to a phenomenon called "russeting" in apples where the outer layers of the fruits are replaced by cork (Tetley, 1930). The subepidermal parenchyma consists of several layers of tangentially elongated cells, which contain carotenoids. These cells were radially oriented in a cross section of the flower. They have divided and enlarged and by a difference in allometric growth, have changed their orientation. Their walls also have thickened, and they are as tightly packed as earlier, in contrast to an apple whose tissues become relatively soft at maturity. The fragrance as well as the coloration of the fruit appear to be localized in the epidermis and in the subepidermal parenchyma. The ground tissue is of loosely arranged parenchyma, well vascularized by a network formed by the anastomoses of the main traces. In a young fruit, the parenchyma cells contain chloro- and chromoplasts. Chloroplasts degenerate at ripening time, and carotenoids are present, but in lesser quantity than in the epidermis and subepidermal layer. In spite of the fact that the fruits of *Chaenomeles* do not soften in ripening, there are many intercellular spaces between the large more or less radially oriented cells of the parenchyma. The fleshy part of the fruit which corresponds to the hypanthium tissue is the exocarp.

In a young ovary, the limit between the hypanthium and the carpels was undiscernable between the circle of ten traces going to the sepals and petals and the circle of five traces on the dorsal side of the carpels. In a mature fruit, patches of sclereids have developed around the median and lateral vascular bundles at the limit of the floral tube and the carpels. These patches become confluent and form an irregular ring of sclereids. There are no sclereids in the flesh of *Chaenomeles* nor are there any in *Malus*. In contrast, there are patches of sclereids or stone cells in the ground parenchyma of the fruit of *Pyrus*, *Cydonia*, and *Docynia*. Inside of the circle of sclereids are the carpels which became cartilaginous early in the development of the fruit. They also are strongly vascularized and possess sclereids. This is considered to be the endocarp lining the locules (McDaniels, 1940). In *Chaenomeles*, the carpels are usually completely fused in the center.

The fruits present a great variation in their shape. More commonly, they are apple-, orange-shaped, or ovoid, when coming from spring flowers; pear- or fig-shaped, when formed on summer or fall inflorescences. Morren (1851) has also observed fruits of *C. speciosa* in the shape of a falciform and ribbed zucchini. As a rule, fruits of *C. japonica* are small and apple-shaped; fruits of *C. cathayensis* are large and ovoid; fruits of *C. speciosa* and of the interspecific hybrids vary in shape and size. A few cultivars (e.g. 'Citri-pomma', lemon-shaped; 'Pyriformis', pear-shaped) have been named for the shape of their fruits. In continental Europe, summer flowers on *Chaenomeles* are infrequent, and have attracted the attention of botanists when they appeared. In New England, where they are of common occurrence, pear-shaped or fig-shaped pedunculate fruits

are found every year on many shrubs. Instead of appearing isolated on old wood, they are clustered on a ramified young shoot. They usually contain fewer ovules than spring fruits, and never mature, being killed by frost.

Independent of their shape, fruits are smooth or ribbed in a few cultivars. Usually there are ten ribs in *C. speciosa* 'Grandiflora Rosea', 'Kermesina Semiplena', 'Phylis Moore', 'Simonii', 'Spitfire', and *C.* × *superba* 'Knap Hill Scarlet'; and only five ribs in *C.* × *superba* 'Ulidia'. This character of having ribs is constant in a cultivar and occurs in fruits formed from spring flowers as well as in fruits formed in the summer and fall.

The fruits of *Chaenomeles* have another peculiarity not found in the closely related genera. They very often terminate in a prominent umbilicus. Other times the calyx becomes accrescent and protrudes as a fleshy rim above the fruit, or it dries up and may persist with the stamens (as in *Malus*, *Pyrus*, and *Cydonia*). The three different kinds of apices may occasionally be found in the fruits of the same shrub. However, the fruits usually offer good characteristics for recognizing some of the cultivars. As the flowers of *Chaenomeles* are similar in all three species, it is interesting to determine the development of these different shapes of fruits.

A swelling of the ovary is evident 10 to 12 days after anthesis. When cut open longitudinally it may be observed that the center where the carpels are fused has increased considerably, and that the ovules have started to enlarge, while the hypanthium is of about the same width as in the flower. At this time there is a natural thinning of the fruits. The flowers which are not pollinated, and certainly many others, fall off. In these, the ovules, instead of increasing, have by now dried up. Soon after, the calyx is shed in one piece by an abscission produced below the insertion of the stamens at the constriction occurring in a more or less gourd-shaped hypanthium. The styles are present and the separated calyx is sometimes retained for a while as a loose ring surmounting the young fruit. The fruit continues to increase in girth, more by enlargement of the center and of the locules than by a thickening of the flesh, which will take place after the locules are nearly full size.

The shape of the apex of the fruits of Japanese Quinces is determined in the first few weeks after pollination, by the abscission or persistence of the calyx, and of the stylar column. The place where the abscission occurs on the column determines the presence or not of an umbilicus. If nothing is left of the column, and if the calyx was shed, the fruit will be terminated by a depression; or if the calyx persists and becomes accrescent, by a hollow protuberance. If a few millimeters of the column remain in the fruit this narrow base will enlarge and form an umbilicus. It may remain sunken in the fruit, be hidden under the accrescent calyx, or be evident by protruding in the cavity left in the hypanthium after its transformation into a pome. The umbilicus is usually hard and fibrous. The cultivar *C. speciosa* 'Umbilicata' has been named for having an umbilicate fruit. Fruits with a very large umbilicus are also found in

*C. speciosa* 'Fireball' and 'Doctor Bang's Pink', and in *C.* × *superba* 'Incendie'. Umbilicate fruits are common in other cultivars, but the umbilicus is not apparent unless the fruit is sectioned longitudinally. Since the column formed by the fused styles is a characteristic of the genus *Chaenomeles*, it is not surprising that umbilicate fruits do not occur in other Maloideae. Occasionally, a shrub shows fruits of different shapes, a condition first observed by Morren (1861). Irregular or malformed fruits may be caused by abortion of the ovules on one side. Ovules after pollination must produce auxins which govern the growth of the flesh. The grooves always correspond to partially or totally empty locules.

The first part of the pome to develop is the core containing the carpels and the ovules. For flowers which were pollinated during the first week of May the core and the ovules have reached approximately their mature size by the beginning of August. Fruits formed in the summer develop much faster. When the core has become cartilaginous the flesh will start to increase. The stage of cell division described by Clements (1935) is replaced by a stage in which the cells enlarge slowly up to the maturity of the fruit.

The skin of *Chaenomeles* fruit is always very thin and completely glabrous. Some of the interspecific hybrids of *C. japonica* possess characteristically sticky skin, which is also a sign of maturity. The skin remains dry in the other two species. The color of the ripe fruits is yellow. Sometimes the showiness of the fruits is the main merit of a cultivar, as in *C.* × *superba* 'George Landis' with orange fruits. This stage of ripening is not reached by all cultivars in the climate of Boston, for the earlier ones mature usually in October. Fruits of *C. cathayensis* need more heat to show color. If fruits do not ripen they remain green, but often are pink or brown on the sunny side. The ripening is also evident in the fragrance of the fruits. The mature seeds are brown. *Chaenomeles* fruits often fall off all at once, especially after a white frost. The fruits may be ripened indoors and formerly, were kept in closets for their pleasant odor. They remain hard and acid until they decompose.

Spring inflorescences contain as many as six subsessile flowers clustered at one point. By natural thinning the number of fruits is usually reduced, but as many as four mature fruits have been observed at one node. The peduncles did not elongate, and they developed a special shape due to the crowding. In *C.* × *superba* 'Boule de Feu' where the peduncles are completely absent, the fruits often surround the supporting spiny twig. This abundance of sessile fruits in the fall is a special aspect of *Chaenomeles* shrubs. The fruits appear on old wood to the ground level. Fruit production is sometimes very heavy, especially in *C. cathayensis* and in *C. japonica* 'Maulei'. *Chaenomeles japonica* is usually the species maturing first, which may be due to its low stature, as is its hardiness.

**Seeds.** The numerous seeds are arranged horizontally in two rows, in each of the five locules. There may be up to 120 in *C. cathayensis*, about 80 in *C. japonica*, and an intermediate number in *C. speciosa* if the ovules

are all fertilized and develop. This is usually not the case, and seeds in full sized fruits number not more than 70 to 80. There appear to be fewer seeds in fruits of interspecific hybrids.

The seeds of *C. japonica* and *C. speciosa* are ovoid and pointed at one end, while those of *C. cathayensis* are wedge-shaped. The testa is coriaceous, dark or reddish brown in the first two species; coriaceous or very slightly mucilaginous, light brown and dull in *C. cathayensis*. In contrast, seeds of both species of *Cydonia* are highly mucilaginous. The raphe and chalaza are apical. The endosperm is lacking. Seeds help in recognizing interspecific hybrids, especially those involving *C. cathayensis*. The seeds of *C. japonica* and *C. speciosa*, in spite of being very numerous in each locule, are more or less ovoid (as in *Pyrus* and *Malus*). In *C. cathayensis*, they take a planoconvex shape by compression with each other (as in *Cydonia*).

**Seedlings.** In *Chaenomeles* the percentage of seed germination is high, and does not appear to be decreased in interspecific hybrids. After a cold period the germination of the seeds takes place immediately. The root ramifies very fast. In five or six days the seedlings, still surmounted by the split testa, begin to emerge above the ground. After shedding the seed coat, the two, rarely three, cotyledons expand and the plumule becomes visible. The young leaves, as well as their stipules, are immediately serrate (also in *Cydonia oblonga*), each serration and interval being marked by a reddish gland, secreting liquid. The glands are sometimes found at a distance of a few millimeters from the edge, on the upper surface of the leaves. The hypocotyl is glabrous while the epicotyl is pubescent.

One or two weeks after germination the seedlings of different species and hybrid groups are very similar. There are, however, a few specific characteristics. *C. cathayensis* and *C. speciosa* appear dull dark green, while *C. japonica* is a shiny yellow-green. The leaves of *C. japonica* and of *C. cathayensis* are glabrous, while *C. speciosa* shows a few trichomes on the midribs of the under surface. The leaves of *C. cathayensis* are more finely and sharply serrate, a characteristic also evident on the young stipules which are more leaf-like on the first few leaves and become reniform on later leaves.

Seedlings of the three species of *Chaenomeles* often show such abnormalities as lobed leaves, cotyledons colored with anthocyanins, or albino leaves. Relatively often, when still in the fruit, seeds rupture and the testa and the cotyledons start to swell, and these seeds continue to grow without requiring a cold period. The seedlings obtained do not show juvenile leaves, but form a rosette of mature looking leaves. However, they do not elongate further without being submitted to a cold period.

**Influence of the environment.** The genus *Chaenomeles*, as shown by its morphology, is extremely plastic. Nearly all organs may present abnormalities, and some of them are so common that they can scarcely be

called aberrations. The plant may be a shrub, or, excluding *C. japonica*, be trained as a small tree. The shoots are of three types, short and long shoots on the crown, and sprouts at the base. The leaves vary a great deal in size, pubescence, and serration. The inflorescences may be of eight different kinds, according to the season. The flowers show all stages from a normal hermaphrodite condition to plants which are predominantly or completely male or female. Unisexual flowers appear usually in the spring and late fall, and a change in sex is possible from year to year in the same shrub. Fruits have two basic shapes, one developed from spring flowers, another on summer inflorescences.

Most of these differences can and do, in fact, appear on the same individual at different seasons. It is striking to observe two or more shrubs of the same clone react in the same manner under the same environmental conditions. For example, a change may occur at the same time in the sex of the flowers, or in the type of inflorescences on adjacent plants. A similar reaction to the climate is not limited to plants belonging to the same clone or even to the same species. Independent of their parental species or hybrid groups, all cultivars from Avery Island, Louisiana, are more spiny than is usual in the genus. In the specimens from Washington, D. C., the leaves are always smaller than on identical cultivars grown in other localities. Fruits are larger when coming from Georgia, but they show abnormally corky and prominent lenticels when grown in the Netherlands. Shrubs in England, usually in late spring, bear the type of inflorescence intermediate between a short and a long shoot. This type is rare elsewhere. These examples show that the genetic make-up of *Chaenomeles* allows the genus a large range of possible responses to the climate, and in part accounts for the selection of cultivars as ornamental plants on six continents.

## CYTOGENETICS

Morphological and taxonomic studies show that the genus *Chaenomeles* comprises three species, namely *C. japonica*, *C. speciosa*, and *C. cathayensis*. These three species cross with each other in every possible way, forming three interspecific bihybrid groups: *C.* × *superba* (*C. japonica* × *speciosa*), *C.* × *clarkiana* (*C. cathayensis* × *japonica*), and *C.* × *vilmoriniana* (*C. cathayensis* × *speciosa*). A fourth interspecific hybrid, *C.* × *californica* (*C. cathayensis* × *superba*) is a synthesis of the three species.

Due largely to confusion of nomenclature but also to the lack of herbarium vouchers, little of the published cytogenetic information on *Chaenomeles* is reliable. Available information, however, does suggest the following:

1. The breeding behavior of *Chaenomeles* is comparable to that of its close relatives in the Maloideae, *Pyrus*, *Malus*, and *Cydonia*.

2. Hybrids within *Chaenomeles* are formed naturally under cultivation and are easily produced by artificial cross-pollination. As variations can be propa-

gated asexually these have been maintained in cultivation for long periods of time.

3. Although polyploids have been suspected, no chromosome counts support this assumption.

There was need, therefore, to repeat the previous work for confirmation; to make additional observations in an attempt to understand or explain the multitude of cultivars described for *Chaenomeles*; and to determine the relationships of *Chaenomeles* to its related taxa.

**Chromosome Studies.** The basic chromosome number of $x = 17$, common to all the Maloideae, was reported by Moffett (1931) for the three species of *Chaenomeles* which have $2n = 34$. He found the chromosomes of this genus to have the same morphology as those in the other genera of the Maloideae. They are small, measuring between one to three micra and, according to Moffett, possess median and submedian constrictions. Moffett's figures of meiosis in *Chaenomeles japonica* (as *Cydonia maulei*) and *C. cathayensis* show secondary pairing of the chromosomes into sexivalents, quadrivalents and bivalents. Sax (1932) thought that the apparent polyvalents might be due to Moffett's technique of sectioning, for they do not appear in smears where, at anaphase, 17 pairs pass to each pole.

In attempting to verify Moffett's work, it was found that meiosis occurs over a period of a few days, usually at the beginning of April, when the buds are 2–3 mm. in diameter on plants grown out of doors, but there is some variation due to the temperature and the cultivar used. Forced flowers proved unsatisfactory for often the stamens fail to develop properly or dry out. The young flower buds were fixed in a solution of one part glacial acetic acid and three parts 95% ethyl alcohol, and kept in the refrigerator until used. To separate the pollen mother cells, the dissected anthers were put into HCl 1 Normal for ten minutes; deposited on a slide and dried; then squashed and mounted in a drop of aceto-orcein and heated slightly. Aceto-carmine was not a satisfactory stain. Because of the small size, the chromosomes were hard to see even in good stamens at the right stage. The preparation had to be examined with the immersion objective. The pollen cells also contained oil droplets about the same size and shape and easily confused with the chromosomes.

All the species and cultivars examined were orthoploid, as in the other Maloideae, which means that they all have the same basic number. Aneuploid series have not been observed in this subfamily. The number of $x = 17$, and $2n = 34$ was confirmed in all the species. It was possible to make counts in seventeen cultivars. As diploid with $n = 17$ were: *C. japonica* 'Pigmani'; *C. speciosa* 'Contorta', 'Nivalis', 'Simonii' and 'Umbilicata'; *C.* × *superba* 'Cameo', 'Corallina', 'Glowing-Ember', 'Mount Shasta', 'Red Chief', 'Roxana Foster', 'Rowallane', and 'Texas Scarlet'; *C.* × *californica* 'California', 'Flamingo' and 'Rosy Morn'. Only one tetraploid with $n = 34$ was found, *C.* × *californica* 'Clarke's Giant Red', which has the largest flowers of all cultivars.

DOCUMENTATION OF CHROMOSOME COUNTS IN CHAENOMELES

Diploid cultivars with $n = 17$.

C. JAPONICA

'Pigmani', Arnold Arb. No. 498–59, Weston, Mass., *Weber*, May 11, 1962 (AAH).

C. SPECIOSA

'Contorta', Arnold Arb. No. 126–42, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Nivalis', Arnold Arb. No. 13022, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

"Simonii', Arnold Arb. No. 178–40, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Umbilicata', Arnold Arb. No. 865–53, Weston, Mass., *Weber*, May 17, 1961 (AAH).

C. × SUPERBA

'Cameo', Arnold Arb. No. 179–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).

'Corallina', Arnold Arb. No. 198–42, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).

'Glowing-Ember', Arnold Arb. No. 766–57, Jamaica Plain, Mass., *Weber*, May 14, 1961 & May 9, 1962 (AAH).

'Mount Shasta', Arnold Arb. No. 176–58, Weston, Mass., *Weber*, May 13, 1961 (AAH).

'Red Chief', Arnold Arb. No. 486–58, Weston, Mass., *Weber*, May 17, 1961 (AAH).

'Rowallane', Arnold Arb. No. 156–52, Weston, Mass., *Weber*, May 9, 1962 (AAH).

'Roxana Foster', Arnold Arb. No. 483–58, Weston, Mass., *Weber*, May 9, 1962 (AAH).

'Texas Scarlet', Arnold Arb. No. 488–58, Weston, Mass., *Weber*, May 14, 1961 (AAH).

C. × CALIFORNICA

'California', Arnold Arb. No. 176–39, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).

'Flamingo', Arnold Arb. No. 512–55, Weston, Mass., *Weber*, May 25, 1960 & May 10, 1962 (AAH).

'Rosy Morn', Arnold Arb. No. 181–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).

Tetraploid cultivar with $n = 34$.

C. × CALIFORNICA

'Clarke's Giant Red', Arnold Arb. No. 751–60, Weston, Mass., *Weber*, May 31, 1961 (AAH).

The only known tetraploid is usually sterile, as are a few other cultivars. Occasionally, it produces fruits containing viable seeds. Since the species of *Chaenomeles* have been shown to be self incompatible, and the shrubs of 'Clarke's Giant Red' were surrounded by cultivars known to be diploid, a few seedlings were grown from one such fruit. As root tip smears are not

dependable, it is necessary to wait for the flower to determine a possible triploid condition.

Cytological investigations do not seem promising in the genus *Chaenomeles*. The pairing cannot be studied well in the genus because of the small size of the chromosomes. Meiosis was found to be normal in the species and in the hybrids, 17 chromosomes passing to each pole at anaphase. This was suspected, as the fertility appears to be normal in hybrids.

**Breeding Behavior.** Flowers of *Chaenomeles* are formed very early in the fall, and open in the spring before the leaves develop, or when the buds are starting to expand. The regular flowers are cup-shaped or flat, and form an easy landing platform for insects. The stigmata seem to be receptive at once and the flowers are proterogynous. The disc is nectariferous although this is not evident out of doors for the flowers are eagerly visited by ants, and nearly all of them are inhabited by thrips which must consume the nectar as soon as it is produced. Nevertheless, if flowers are kept in the refrigerator for a few days in a closed jar, nectar appears as droplets on the disc. Its taste is sweet and its peculiar odor resembles that of apples, or of maple sap. Otherwise, the flowers have no scent. The young unfolding leaves also produce liquid through the glands at about the same time. The stamens in two rows are incurved in the buds. The stamens of the outer row have straightened up by anthesis and are ready to shed pollen after a few hours or within one or two days after the flowers open. The inner row of stamens will, in turn, straighten and start to shed pollen one or more days after the stamens of the outer row. At this time, flowers are visited by honey bees, and occasionally by bumble bees. Japanese Quinces are listed by some nurseries as melliferous plants. If the weather is hot and sunny, the flowers may drop the still turgid petals while the outer row of stamens is shedding pollen. By the end of anthesis, anther sacs have tipped over and stamens become slightly versatile. When empty, they change from yellow to brown.

In the spring, each flower lasts about a week, but the blooming period is longer, for flowers start to open close to the ground (which warms up earlier) and follow later along the higher branches. In spring inflorescences containing several flowers, the one in the center usually opens first, gradually followed by the others. The terminal flower is the youngest in the racemes or panicles formed in the summer, and usually is the last one to open.

When ripe, the fruits do not persist long on the shrubs. They often drop all at once, probably due to frost. When the fruits are on the ground (but sometimes while still on the shrubs) they are opened by birds seeking the seeds. The flesh is very acid and does not seem to be eaten. The seeds are also eagerly collected by rodents. A burrow (of rats?) was observed under a shrub of Japanese Quince and split open fruits were carefully piled up as refuse on both sides of the entrance. No seeds were left on the rejected cores, but were probably stored underground.

Most likely, the seeds of *Chaenomeles* are dispersed by birds and small animals, when gathering food for winter preserves. A shrub, as a garden escape, was observed by Fernald in a hedge at Barnstable, Mass. Japanese Quinces are also known to become naturalized in Japan and Korea. In cultivation, no seedlings have been observed close to mature shrubs. This may be due to the numerous animals eating the seeds. Flocks of pigeons have been observed repeatedly near Japanese Quinces when the fruits were on the ground. It is difficult to believe that large seeds, often already breaking the seed coat inside the fruits, can pass undigested through the intestinal tract of a bird, but enough must be lost by the animals collecting the seeds to ensure reproduction in the wild.

From old observations, *Chaenomeles* was suspected to be self incompatible but the possibility of apomixis had to be investigated since it is of frequent occurrence in *Malus* and other genera of the Maloideae. It is recorded that *C. speciosa*, when introduced into Europe at the end of the eighteenth century, did not bear fruits for many years. At that time, it was believed that the temperature was not adequate for fruit production. Shrubs often were kept in greenhouses but still did not form fruit. When Japanese Quinces became common, and many varieties were grown in adjacent areas, fruits appeared in any climate. The early reports of no fruit development were certainly due to self incompatibility as subsequent experiments seem to have demonstrated.

Apomixis includes reproduction in which embryos (and seeds) are produced asexually (agamospermy). Simple experiments involving the bagging of flowers or the isolation of plants may give the first indication of the presence or absence of this phenomenon. Colby (1929) bagged various cultivars of *Chaenomeles* and reported that except for *C. speciosa* 'Grandiflora', no fruits were produced. Similar experiments were performed for this study on *C. speciosa* 'Early Apple Blossom'; *C.* × *superba* 'Columbia', 'Sunset', and 'Superba'; as well as on *C.* × *californica* 'California'. No fruits were produced. The explanation of fruit production in one cultivar is not clear. The flowers of *Chaenomeles* are visited by ants and extremely small insects attracted by the nectar present inside the floral cup at anthesis and along the unfolding leaves. It is possible that these small insects penetrated the bag placed around a branch of *C. speciosa* 'Grandiflora'. A word of caution must be expressed. The position of the flower clusters of *Chaenomeles* on old wood, requires the shoot system to be enclosed in plastic or paper bags. Artificial conditions of heat and moisture are evident in the bag and are detrimental to the young foliage and perhaps to the flowers. However, in most cases sufficient normal shoot development was observed to eliminate this factor in accounting for the lack of fruit production.

A second test of apomixis and self incompatibility was made by the observation of isolated plants without bagging, and insect pollination limited to natural selfing. A shrub of *C. speciosa* located near the Harvard Law School was observed for two years during which it did not produce fruits. The closest Japanese Quinces, members of the Superba group,

are in the Cambridge Common, a distance of about 200 meters. In the spring of 1962, flowers of *C.* × *superba* were used to pollinate, by hand, a few flowers of the isolated specimen of *C. speciosa* at the Law School. The artificially pollinated flowers were tagged and all of them produced fruits. No fruits were formed from flowers not cross pollinated by hand. The seeds were sown, and all the seedlings showed traces of hybridization between *C. speciosa* and *C.* × *superba*. In another experiment, to serve as a control, a shrub of *C.* × *superba* 'Knap Hill Scarlet' known for its fruit production was transplanted from the shrub collection of the Arnold Arboretum in Jamaica Plain to an isolated spot in Cambridge. It bloomed abundantly in its new location during the spring of 1962, but in spite of numerous bees that visited the flowers, not one fruit was formed.

The same condition occurred in a plant of *C. speciosa* 'Tani-no-Yuki' and one of *C.* × *superba* 'Otto Froebel' moved into the greenhouse. In the absence of pollinators to effect cross pollination, no fruits were produced. A few flowers were self-pollinated by hand and these also failed to develop fruits. However, a few flowers were cross-pollinated between the two varieties and all produced fruits with fully developed ovules. In addition to the fruit formation, the pistils of these self- and cross-pollinated flowers were also observed. The styles were collected from one to three days after hand pollination; dipped for two days in Gentian violet and then mounted in lactophenol. Under a microscope, it was possible to examine the growth of the pollen tubes.

Self-pollinated flowers of *Chaenomeles* have been observed to have aberrant pollen development. When pollen is placed on the stigmata there may be complete failure of pollen tube development or the tube may develop and not penetrate the stigmatoid or stylar tissues. In such flowers there may be a slight swelling of the hypanthium but the resulting small fruits turn yellow and fall within a few weeks. Sections of such fruits show no ovule development.

In the collections of the Arnold Arboretum many cultivars of *Chaenomeles* are grown side by side in rows. With this abundance of plants fruit production is usually heavy, although some cultivars remains sterile year after year. In contrast, in the Boston suburbs isolated plants may be found as ornamental shrubs in gardens, which rarely fruit or produce malformed fruits containing a reduced number of seeds, but never less than four. There seems to be no parthenocarpy as in *Malus*, where fruits of normal appearance may be formed without seeds.

Hall (1931) studied the problem of fruit failure in the apple and recorded that the fruit production of a given variety may be inconsistent. A variety which is self sterile under one set of conditions may be self fertile under another. Self incompatibility may be the result of genetic factors but environmental factors may also influence fruit production.

**Hybrids.** Intergeneric hybrids are of common occurrence in the Maloideae, but none are recorded with *Chaenomeles* as one of the parents in spite of the common chromosome number $2n = 34$, and the same

chromosome morphology. Crosses between the two species of *Cydonia* and species of *Chaenomeles* were unsuccessful in several attempts. Crosses with other genera should be tried. The three species of *Chaenomeles* have been shown to be completely interfertile under cultivation and there seems to be no reduction of fertility in subsequent generations of hybrids. This should, however, be tested statistically. Genetically, *Chaenomeles* appears to be a distinct taxon.

Self incompatibility in ornamental plants favors the production of hybrids by natural and artificial means. There was very little variation in *Chaenomeles* during the first twenty years after the introduction of *C. speciosa* from Japan into Europe, in 1796. During this period, all plants were probably propagated asexually from the first shrub introduced at Kew Gardens, as no fruits were produced. One variety with blush flowers, called white, existed very early, and may have been a separate introduction. It was only after 1830 when von Siebold returned from Japan with many color forms of *C. speciosa* that varieties were developed in Japanese Quinces by the selection of seedlings. The colored forms, grown side by side, certainly crossed naturally. Before the introduction of any other species, numerous selections had been made in *C. speciosa* on the basis of variation in flower color, in number of petals, in the shape of the fruits, and in the size of the plants. The selections made over a century ago were the start of clonal lines which, through asexual propagation, are still grown in many gardens.

In 1869, a second species, *C. japonica*, was introduced into Europe. This species was distributed to gardens where *C. speciosa* was planted, and from the beginning set fruits. *C. japonica* was reproduced by seeds, and was thought to breed true. Very soon, numerous color forms appeared in the progeny of this species. They were considered varieties, but later all proved to be natural hybrids with *C. speciosa*. Such was the origin of *C.* × *superba*. In recent years, numerous cultivars have been added to this group by selection, or by deliberate crossing of the two parental species.

*C. cathayensis*, introduced into Europe around 1880, appears to be very uniform, but more observations must be made on this species before its breeding behavior can be ascertained. This species is closest to *Cydonia* which contains two species known to be self compatible. The hybrid groups *C.* × *clarkiana*, *C.* × *vilmoriniana*, and *C.* × *californica* were produced by hand pollinating flowers of two different species, or, the latter by pollinating flowers of an interspecific hybrid by a third species. The progeny of the interspecific hybrids proved to be fertile with other hybrids, or with any of the parents. As a result, *Chaenomeles* has an amount of variation unequalled in the other genera of the Maloideae partially due to backcrossing and introgression.

The taxonomic treatment of several hundred cultivars of *Chaenomeles* presents a significant problem. The horticulturist would accept a grouping based on the color of the flower, the form of the flower, single, semi-double or double, or perhaps a classification based on hardiness, fruit

shape, or habit. The botanical approach requires recognition of the parent species and suggests that the cultivars be treated as a hybrid swarm. The fundamental information on the species was obtained by a study of herbarium specimens collected in the localities where the species are not found together. *C. japonica* is restricted to Japan where no other species is native. *C. speciosa* and *C. cathayensis* are from China. The sparse collections and the lack of data on their distribution and ecology do not indicate whether they grow together within their sympatric range, but no hybrids of these species have been recorded in China, and none were found among the herbarium specimens. Information on individual variation within a pure species was also available from shrubs grown from seeds of wild plants.

The morphological variation of the species is extreme and it was, therefore, impractical to apply the usual techniques of scatter diagrams, ideographs or hybrid indices for this reason, and because of the numerous cultivars of the Californica group which are hybrids of not two but three species. A different method had to be devised to analyse each of the more than 300 named cultivars produced by variation within three species, by simple crosses in four combinations, and by backcrosses with subsequent asexual propagation. Anderson's techniques inspired the method used in this study.

Herbarium specimens of cultivars were gathered from different localities to observe the differences due to the environment. These specimens were supplemented by colored drawings of fresh flowers. The drawings, more reliable than colored photographs, allowed a comparison of characters important to the horticulturist, but not easily preserved in dried specimens. Since numerical evaluation could not be used with trihybrids, the usual scoring was replaced by attributing each morphological character of the cultivar, such as habit, twig, leaf, flower, and fruit to the species it resembled most. It was found that the different organs usually tended to be closer to the type encountered in one of the species, perhaps because of the presence of linked genes, or at least of several genes on a single chromosome affecting the same organs. When the characters were intermediate, this was indicated. From the results of the listing, each cultivar was attributed to a species, or to a hybrid group, when possessing characteristics of more than one species. The records of the parentage of crosses made by a few nurserymen were generously supplied and in most cases substantiated the recording technique. On several occasions cultivars, supposedly authentic, could not have been produced by the parentage suggested, and indicated an error in the identification of the cultivar, or one of its parents. Many cultivars in *Chaenomeles* are known to be backcrosses. Others suggest that introgression has advanced far in the Japanese Quinces. As Anderson stated "In the second generation of hybrids and in backcrosses there will be various and multitudinous recombinations of flower color, shapes and heights and no two plants will look very much alike." This explains why so many cultivars can be produced from three basic species.

The relative ease with which characteristics of habit, twig, leaf, flower, and fruit could be attributed to the parents of one species or another, permits identification of the parents of a hybrid, and also prediction as to the progeny of the cross. After the intercorrelated characters were sorted, it was possible to list those characters tending to appear together. For example, a cultivar with orange petals always has crenate leaves, warted twigs, and is of medium size. These characters come from its parent, *C. japonica*. Leaves with serrations terminated by an awn-like tip usually show some pubescence on the under surface, both characters coming from *C. cathayensis*. Having so many hybrids of known parentage, it was possible to recognize the characteristics which tend to be expressed.

The members of the Superba group, *C. japonica* × *speciosa*, usually are shrubs of intermediate size and branching. The twigs have the warting of *C. japonica*. The leaves are intermediate between the leaves of the two species, or more japonica-like as far as the color (dark green in *C. speciosa*, yellow-green in *C. japonica*), pubescence, and serration are concerned. The flowers have the wide range of color of *C. speciosa*, with the addition of pure orange found only in this group as a combination of the salmon pink of *C. japonica* with the red of the other species. Fruits are intermediate in size and perhaps in shape, but are closer to those of *C. japonica*. The sticky skin in many hybrids is also derived from *C. japonica*. The seeds, which are very similar in shape and size, may be differentiated only by the shiny testa of *C. japonica*, often present in seeds of the hybrids, versus the dull testa of *C. speciosa*.

The three cultivars of the Vilmoriniana group, *C. cathayensis* × *speciosa*, are intermediate as far as characteristics of the habit and twigs are concerned, but show the influence of *C. cathayensis* in the other characters.

These two hybrid groups show that in a cross of *C. japonica* × *speciosa*, the characters of *C. japonica* tend to be expressed over those of *C. speciosa*; in a cross of *C. cathayensis* × *speciosa* the progeny will look more like *C. cathayensis*. It is interesting to compare these observations with the characters of the cultivars of the Clarkiana group, *C. cathayensis* × *japonica*. Although two cultivars only are in this group, they are both intermediate in all their parts and neither parent dominates the other.

An analysis of the numerous cultivars of the Californica group, *C. cathayensis* × *superba* reveals mostly intermediate characters, those of *C. cathayensis* tending to be expressed in the shape and size of the shrubs, in the spines, and often in the fruits. The flowers encompass the range of color found in *C. speciosa*, but are often of two tones of pink, brighter but very much like the flowers of *C. cathayensis*.

These results, obtained from a study of the existing cultivars, may serve as a guide for the plant breeder wanting to produce a certain type of shrub. Size is certainly due to multiple genes, being in the range of the size of the parental species. Branching and spininess of *C. japonica* tend to be expressed when crossed with *C. speciosa*. In a cross including *C. cathayensis* as one parent, the shrub will look more like *C. cathayensis* than any other. The warting of *C. japonica* is always present in its pro-

geny, and is an important character in detecting hybridization with this species. *C. japonica* leaves, characterized by glabrescence and crenate teeth, may be contrasted with the leaves of *C. cathayensis*, showing serration, terminated by an awn-like tip and abundant fulvous tomentum on the under surface at maturity. The leaf characters of *C. japonica* and of *C. cathayensis* again, tend to be expressed over those of *C. speciosa*. Interspecific hybrids, including the two dominant species, possess leaves intermediate in size, serration, and pubescence between those of the parents. The flowers are usually intermediate, taking up the range of color of the species with the largest range. A new color, orange, has appeared in hybrids by combination of pigments separately present in *C. japonica* and *C. speciosa*. In hybrids including *C. cathayensis*, flowers are often bicolored as in this species. The fruits tend to be intermediate in shape and size between those of the two parents; the ovoid shape of *C. cathayensis* appearing often in its hybrids. In the seeds, the wedge-shape of *C. cathayensis* is expressed over the unspecified shape of *C. speciosa* (found also in *C. japonica*), while seed characteristics of *C. japonica* dominate those of the others in shape, size, and the nature of the testa. To these morphological characters may be added the physiological one of hardiness. In a cross between a hardy species and one which is not, the lack of hardiness, probably due to multiple genes (as present in *C. cathayensis*) is usually expressed.

This survey of the morphological characters and behavior of the different cultivars belonging to the three species, and to the four hybrid groups shows that *C. cathayensis* and *C. japonica* are two well defined species. Their morphological characters are easily recognized, and are evident in their progeny. This is not the case with *C. speciosa*, which is less specialized and does not possess characters not present in some degree in the other two species. This was evident when preparing the key to distinguish species and hybrid groups. The separation was found to be difficult between the cultivars belonging to *C. speciosa* and those of *C.* × *clarkiana*, a hybrid between *C. cathayensis* and *C. japonica*.

Evreinoff (1937) quotes Pachkevitch (1930) as saying that he believed *C. lagenaria* to be a hybrid between the other two species. The nomenclature is so confused in Evreinoff's paper that it is not possible to ascertain whether *C. lagenaria* in his sense means *C. speciosa* or *C. cathayensis*. Unfortunately, Pachkevitch's treatise on pomology, in Russian, could not be obtained. His idea of the origin of one of the species of *Chaenomeles* by hybridization of the other two is appealing. It would explain why *C. speciosa* has no morphological character and range of its own, and why it is by far the most variable species in cultivation as well as in a native state. It may also suggest an explanation of the fact that the three species are still so closely related that they cross freely when grown in gardens. *C. japonica* is native only in Japan, *C. cathayensis* and *C. speciosa* probably occurring in different habitats in the region of Yunnan, China, did not develop reproductive isolation because other isolation mechanisms are present to keep them apart in the wild.

[*To be concluded*]

# THE GENERA OF CELASTRALES IN THE SOUTHEASTERN UNITED STATES [1]

GEORGE K. BRIZICKY

THE ORDER CELASTRALES, as delimited here, includes the families Celastraceae, Hippocrateaceae, and Aquifoliaceae, as well as several other allied families (e.g., Siphonodontaceae, Stackhousiaceae) not represented in the southeastern United States. The Staphyleaceae, usually regarded as members of either Celastrales or Sapindales, are excluded from both these orders, and will be treated within Cunoniales (or Saxifragales *sensu lato*), where they seem to belong (cf. C. G. G. J. van Steenis, Fl. Males. I. **6**: 49. 1960).

## CELASTRACEAE R. Brown in Flinders, Voy. Terra Austr. **2**: 554. 1814, "Celastrinae," nom. cons.

(STAFF-TREE FAMILY)

Usually glabrous trees or shrubs, rarely woody vines, sometimes gutta-percha [or rubber] bearing; nodes unilacunar. Leaves simple, membranaceous to coriaceous, opposite or alternate [rarely minute or rudimentary], petiolate, deciduous or persistent; stipules minute, usually caducous. Inflorescences axillary and/or terminal, cymose (usually dichotomously branched) or racemose, or the flowers solitary and/or fascicled in the leaf axils. Flowers small, regular, hypogynous, perigynous, or semi-epigynous, bisexual or unisexual by abortion (the plants then monoecious or dioecious), pediceled (except *Gyminda*). Sepals 4 or 5, small, connate about half of their length or more, or nearly distinct, usually imbricate.

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through those in volumes 40–44 (1959–1963). The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Carroll E. Wood, Jr., for his many valuable suggestions; to Harry Ahles, George R. Cooley, Wilbur H. Duncan, and James W. Hardin, for checking herbarium records on the distribution of some genera of Celastraceae, especially *Paxistima*, in the southeastern United States; and to Mrs. Gordon W. Dillon, for her help in preparation of the manuscript. The illustration of *Euonymus* was drawn by Dorothy H. Marsh, in part from fresh fruiting material sent by R. B. Channell.

Petals 4 or 5, distinct, inserted under the disc, usually imbricate. Stamens 4 or 5 [very rarely 8–10], distinct, alternipetalous, inserted under or on the disc at its exterior margin, reduced or wanting in ♀ flowers; filaments short; anthers basi- or dorsifixed, introrse, longitudinally dehiscent. Nectariferous disc intrastaminal, usually conspicuous, variously shaped, rarely wanting. Gynoecium syncarpous, 2–5-carpellate, rudimentary in ♂ flowers; stigma single, ± lobed, or stigmata 2–5; style single or wanting; ovary superior, distinct or ± immersed in and sometimes fused with the disc, or semi-inferior, 2–5-locular; placentation axile; ovules usually 2, more rarely 1 or 4–6 [to many] in a locule, pendulous from the top or ascendent from the base of the placenta, anatropous, usually apotropous, 2-integumented. Fruit a loculicidal [rarely septicidal] capsule or a drupe [berry or samara], (1)2–5-locular, the locules 1– or 2–6-seeded. Seeds often arillate; endosperm present [rarely absent]; embryo straight, axile; cotyledons large, foliaceous, often green; radicle short, superior or inferior. TYPE GENUS: *Celastrus* L.

A primarily pantropical family of 50–55 genera and over 800 species, extending with several genera into the temperate zones, to which a few are restricted. Six genera occur in our area. The genus *Paxistima* Raf. (also incorrectly spelled *Pachystima* or *Pachistima*; see Wheeler, p. 293) is excluded from the flora of the southeastern United States.[2]

Pollination by insects seems to be the rule. Data on floral biology and anatomy, as well as on embryology are sparse, pertaining to a few genera and species. Chromosome counts made for four genera (eight species) are $2n = 32$ and 64, 46, and 80. Though sparse, these numbers may suggest that both aneuploidy and polyploidy have been of importance in the evolutionary development of Celastraceae.

The family is closely related to Hippocrateaceae and Aquifoliaceae. A relationship with Siphonodontaceae and Stackhousiaceae has also been assumed (Takhtajan).

[2] The occurrence of *Paxistima Canbyi* Gray in North Carolina was first recorded by Chapman (Fl. So. U.S. ed. 2. 613. 1889) on the authority of M. A. Curtis. Apparently on the same basis the species was included by Small (Fl. SE. U.S. 735. 1903; Man. SE. Fl. 818. 1933), who repeatedly mentioned the occurrence of the species in North Carolina. Massey (1940) was not able to verify this but concluded that "considering the distribution of limestone, this species should be sought more extensively in southern Ohio, northern Kentucky, northeastern Tennessee, and possibly in western Maryland and south central Pennsylvania." No collections of *P. Canbyi* from North Carolina have been available until J. W. Hardin recently investigated a report of the species in Mitchell County, North Carolina. He found (1963) that this species was introduced, apparently from West Virginia, into the Green & Taylor nursery, now abandoned; the plants are growing well and the population is expanding, but still without competition from the native vegetation; it remains to be seen whether the plants survive the invasion of the forest in the years to come. "In the meantime, although *Pachystima Canbyi* is now thriving in this location in western North Carolina and without constant cultivation, we still cannot call it a definite member of the native southeastern flora."

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## Key to the Genera of Celastraceae

General characters: *woody plants with opposite or alternate leaves with minute, usually caducous stipules; flowers small, bisexual or unisexual, 4- or 5-merous, usually with a conspicuous nectariferous disc, in axillary dichasial cymes or few-flowered fascicles, more rarely in terminal thyrses; stamens alternipetalous; ovary usually superior, 2–5-locular, sometimes ± immersed in the disc, the placentae axile, the ovules usually 2 or 1; fruit either a loculicidal capsule with arillate seeds or a drupe.*

A. Plant scandent, woody, dextrorsely twining; leaves alternate; flowers in terminal or axillary raceme-like thyrses; capsule subglobular, ca. 1 cm. in diameter, orange or yellow; seed covered with a scarlet aril. 2. *Celastrus.*
A. Plant nonscandent, shrubby, sometimes prostrate or creeping, or arborescent; flowers in axillary dichasial cymes or fascicles.
  B. Leaves opposite; flowers in axillary dichasially branched cymes.
    C. Plant deciduous, leaves membranaceous (rarely subcoriaceous); anther-halves diverging; ovary locules 2–6(10?)-ovulate; fruit a 3–5-lobed, -valved, sometimes tuberculate capsule; seed covered with a scarlet aril; occurring north of central Florida. 1. *Euonymus.*
    C. Plant evergreen, leaves thin-coriaceous; anther-halves parallel; ovary locules 1-ovulate; fruit a small drupe; seed exarillate; subtropical Florida.
      D. Flowers slender pediceled, 2-bracteolate at base of pedicel, bisexual; sepals connate nearly half their length; stigmata 4, narrow, spreading, raised on a short style; ovary 4-locular; ovule ascendent from the base of the placenta; drupe red,

obliquely obovoid, 3–6 mm. long, excentrically crowned with a persistent style. ..... 4. *Crossopetalum.*

D. Flowers sessile in the forks of dichasia, 2-bracteolate just under the calyx, unisexual, the plants dioecious; sepals nearly distinct; stigmata 2, broad, sessile; ovary 2-locular; ovule pendulous from the top of the placenta; drupe black or dark blue, ellipsoidal, 6–8 mm. long, crowned with the persistent stigmata. ..... 5. *Gyminda.*

B. Leaves alternate; flowers in axillary few-flowered fascicles or solitary.

E. Leaves fleshy-coriaceous, with indistinct venation on the upper surface; flowers 5-merous, with a 3-carpellate gynoecium; fruit a red ellipsoidal to obovoid capsule, 8–12 mm. long, dehiscing by 3 valves; seed arillate. ..... 3. *Maytenus.*

E. Leaves thin-coriaceous, conspicuously veined on the upper surface; flowers 4-merous, with a 2-carpellate gynoecium; fruit a scarlet subglobular drupe 5–6 mm. in diameter, containing 2 stones; seed exarillate. ..... 6. *Schaefferia.*

## Subfamily CELASTROIDEAE

### Tribe CELASTREAE

### 1. **Euonymus** Linnaeus, Sp. Pl. 1: 197. 1753; Gen. Pl. ed. 5. 91. 1754.

Deciduous [or evergreen] shrubs [sometimes climbing by aërial rootlets] or trees, with green, usually quadrangular branchlets [sometimes corky ridged or warted]. Leaves opposite [rarely whorled or alternate], membranaceous [to coriaceous], crenate-serrate or serrulate, with gland-tipped teeth [rarely prickly or entire], usually petioled; stipules caducous [rarely persistent]. Inflorescences axillary [and terminal], simple or compound dichasially branched (1)3–15(31)-flowered peduncled cymes with minute caducous bracts. Flowers 4- or 5-merous, hypogynous (or semi-epigynous?), bisexual (rarely also unisexual by abortion, the plants then polygamo-monoecious or -dioecious). Sepals connate about half their length. Petals ovate-orbicular to suborbicular [to linear], sometimes shortly clawed, greenish white to purple [or greenish yellow]. Stamens inserted on the margin of a conspicuous fleshy usually 4- or 5-lobed nectariferous disc; filaments subulate, very short [more rarely ± elongate, or wanting]; anthers basifixed, broad, the anther-halves connivent [or confluent] at apex and much divergent to subhorizontal toward the base, 2[1]-locular at anthesis, dehiscing by 2 lateral [or 1 continuous subapical] slit. Gynoecium 3–5-carpellate; stigma small, indistinctly 3–5-lobed; style short, stoutish; ovary superior (or semi-inferior?), [2]3–5-locular, ± immersed in, except the top, and fused at base with the disc; ovules 2–6(10)[–12] in a locule, ± ascendent or rarely pendulous, superposed or collateral [or in 2 rows], apotropous, the nucellus thin. Fruit a leathery capsule, usually pink to red or purple, subglobular or oblate [or obovoid, obconical or obpyramidal], smooth or "tuberculate" [or echinate], usually [2]3–5-locular, -lobed [-angled or -winged, or rarely round in cross-section], and -valved; locules 2–6(10?)-seeded. Seed partially or com-

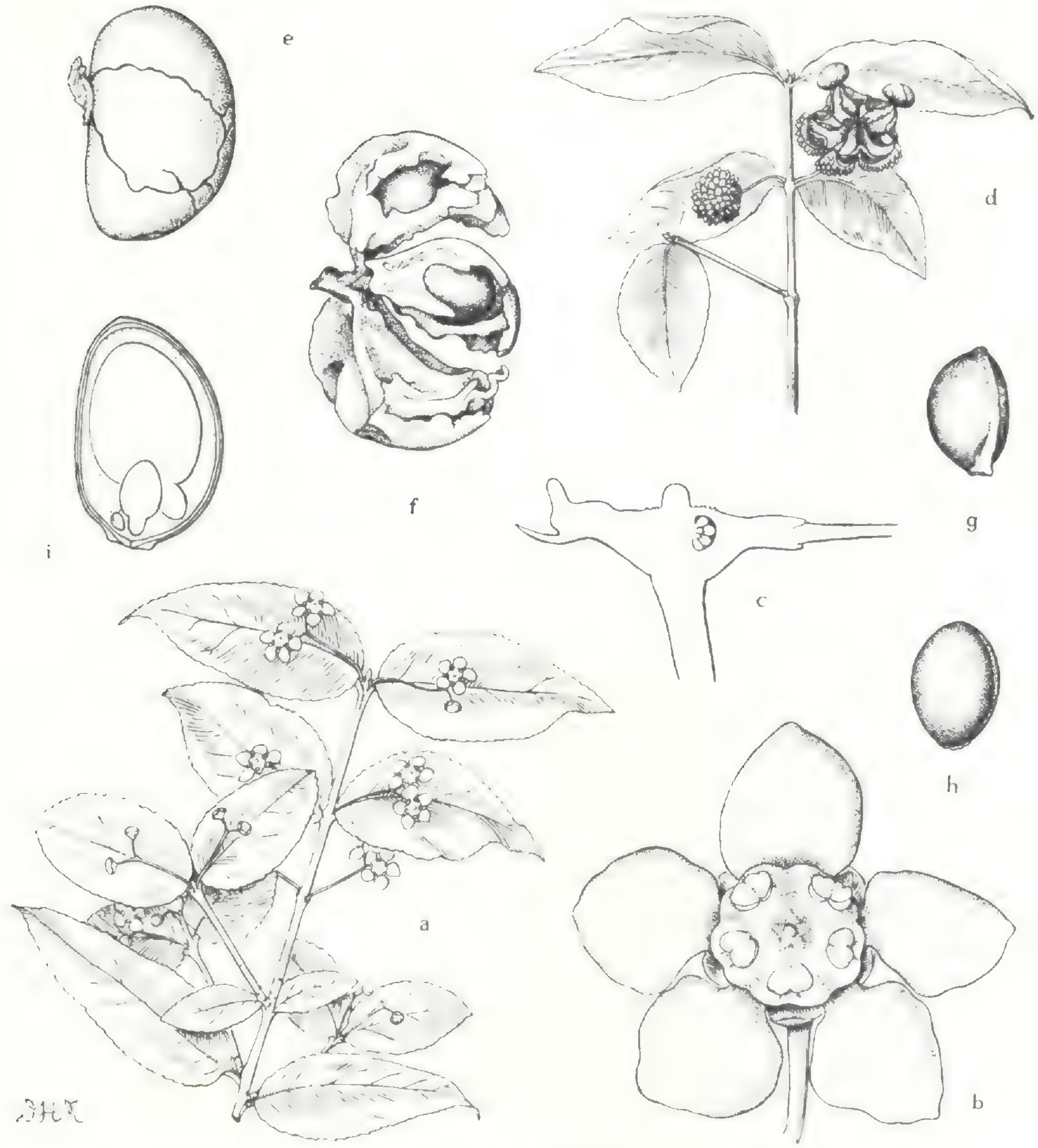


FIG. 1. **Euonymus.** *E. americanus*: a, flowering branchlet, from above, × 1; b, flower, × 10; c, flower in diagrammatic vertical section, to show insertion of petal and stamen (anther removed) and ovary immersed (except papillate top) in disc, × 16; d, fruiting branchlet bearing incompletely developed capsule and open loculicidal capsule with two clusters of seeds, × 1; e, cluster of four arillate seeds from a single locule, arils squeezed together, × 6; f, three lower seeds of same cluster separated to show varying development of aril, × 6; g, h, two views of seed, showing raphe, the micropyle below, × 6; i, seed in diagrammatic vertical section in plane of raphe, showing two seed coats and three of four embryos embedded in endosperm (stippled), × 12.

pletely covered by a scarlet or orange aril; seed coat leathery, orange- or reddish-brown [to black, or whitish]; endosperm abundant, fleshy; embryo large, the cotyledons roundish to oblong, usually green; the radicle inferior or superior. LECTOTYPE SPECIES: *E. europaeus* L.; see N. L. Britton, N. Am. Trees 630. 1908. (Name from Greek, *eu*, good, and

*onoma*, name, i.e., of good name, famous, apparently applied ironically to the genus, the plants having had the bad reputation of poisoning cattle.) — SPINDLE-TREE.

A genus of nearly 180 species of the North Temperate Zone and the Tropics, concentrated in eastern Asia, a few in Europe, Africa, Madagascar, and Australia, completely absent in South America and the West Indies; five to seven unsatisfactorily known species in Central America (south to Costa Rica), four in the United States, and three in our area. Blakelock's classification, which recognized subgenera EUONYMUS and KALONYMUS Beck emend. Blakel. with six sections and 14 series, is followed here. All American species belong to subg. EUONYMOUS, characterized by small, ovoid, acute winter buds, filamented (*vs.* subsessile) stamens, anthers two-locular at anthesis and dehiscing by two distinct slits, and unwinged capsules. The sections are based primarily on the shape and degree of lobation and the character of the surface of the capsules.

Section EUONYMUS (§ *Biloculares* Rouy & Fouc. emend. Blakel.) includes about 70 Old World and two (or three) American species, all with two-ovulate locules and smooth fruits. The primarily northeastern American *Euonymus atropurpureus* Jacq., wahoo or burning bush, a large shrub or small tree with four-merous purple flowers, occurs in thickets along streams and in rich damp woods from southern Ontario to southern Minnesota, southeastern South Dakota (and locally in Montana), south to Nebraska, Kansas, Oklahoma, northeastern Texas, Arkansas, and Tennessee, with scattered stations in North Carolina, Georgia, Alabama, Mississippi, and northernmost Florida (Gadsden County). *Euonymus occidentalis* Nutt. ex Torr., differing in part in its five-merous flowers, occurs from Washington to California. *Euonymus europaeus*, $2n = 64$, with greenish-white petals and 3–5-flowered inflorescences, often grown as an ornamental, has been recorded as naturalized in at least the northeastern United States.

Primarily of eastern Asia, sect. ECHINOCOCCUS Nakai emend. Blakel., characterized by five-merous flowers (in our species), 4–6(–10?)-ovulate locules, and tuberculate fruits, includes five North American species, two in our area. *Euonymus americanus* L. (including *E. angustifolius* Pursh), strawberry-bush, $2n = 64$, an upright or straggling (very rarely creeping) ± stoloniferous shrub with rather variable, rarely obovate thickish leaves, densely minutely pustulate branchlets, flowers about 1 cm. in diameter, distinctly clawed petals, and (3-)5-locular capsule is common throughout much of our area.[3] It occurs in rich lowland woods and thickets, in ravines

[3] Two poorly known variants of uncertain taxonomic status have been described as varieties of *Euonymus americanus*. The var. *angustifolius* (Pursh) A. Wood, with narrowly lanceolate to sublinear leaves (as against lanceolate or ovate, rarely obovate, ones in var. *americanus*) was described from Georgia and is also known from at least North Carolina and/or Tennessee (French Broad River), and northernmost Florida (Apalachicola River). The var. *sarmentosus* Nutt., a prostrate, usually creeping shrub, rarely seen with flowers (Meehan), seems to be of rare occurrence in some parts of our area (at least in Tennessee and Arkansas). Perhaps it represents a distinct

and bottoms, and on river bluffs from New York west to southern Illinois and southeastern Missouri, south to eastern Texas and Highlands County, Florida. The primarily northeastern American *E. obovatus* Nutt., running strawberry-bush, a creeping shrub with upright flowering shoots 3–6 dm. high, thin, usually obovate leaves, smooth branchlets, flowers 6–7 mm. in diameter, nonclawed petals, and usually three-locular capsules, reaches its southern limits in Tennessee and southwestern North Carolina, where it occurs in rich, moist or dry woods, on moist shaded banks, or on rocky bluffs.

The Asiatic *Euonymus alatus* (Thunb.) Sieb., of sect. MELANOCARYA (Turcz.) Nakai emend. Blakel., an ornamental shrub with spreading, usually corky-winged branches and smooth four-parted capsules, has become established locally in at least Connecticut, West Virginia, and Kentucky.

Flowers of the genus usually are bisexüal and proterandrous, but the occasional occurrence of unisexual flowers (the plants consequently monoecious or dioecious) has been recorded at least in European species. Hymenoptera and Diptera, especially short-tongued bees and flies, seem to be the main pollinators. The attractive arillate seeds are dispersed by birds. Seeds in many (perhaps most) species have a long dormant period, requiring stratification before germination. Apomixis (adventitious polyembryony from the inner integument of the ovule, perhaps rarely from the endosperm) is known in *Euonymus latifolius* (L.) Mill., *E. americanus*, and *E. alatus*, as well as in several eastern Asiatic species. Fertilization is necessary for the development of adventitious embryos.

Berkeley, on the basis of four species, interpreted the "broad flat structure surrounding the ovary" [the disc] as a floral tube and considered the ovary to be semi-inferior, the flowers semi-epigynous. The occurrence of fibriform vessel elements in the wood of the stem and of secretory cells (sacs) containing gutta-percha in the phloem of the roots (and sparingly of the axis) is notable.

Reported chromosome numbers (four species) are $2n = 32$ and 64. The lower number was found in *Euonymus japonicus* Thunb. and *E. Fortunei* (Turcz.) Hand.-Mazz., representing the presumably primitive sect. ILICIFOLIA, while the higher pertains to *E. europaeus* and *E. americanus*, of two presumably advanced but not closely related sections.

The genus is closely related to the West Indian *Torralbasia* Krug & Urb. and the New Guinean *Xylonymus* Kalkm.

Many species are grown as ornamentals. At least *Euonymus verrucosus* Scop. and *E. europaeus* are cultivated in the Soviet Union as sources of gutta-percha. The seeds (containing the glucoside evonosid, a heart poison) and the vegetative organs of at least the European species and *E. atropurpureus* are said to be poisonous.

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population of the species which seems to be more pronouncedly stoloniferous than the typical variety. In the study of the variants the common occurrence of apomixis (adventitious embryony) in *E. americanus* should be taken into consideration.

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2. **Celastrus** Linnaeus, Sp. Pl. 1: 196. 1753; Gen. Pl. ed. 5. 91. 1754.

Scandent, usually dextrorsely twining shrubs with alternate, elliptic to suborbicular or obovate, serrulate to serrate [or subentire], deciduous

[rarely persistent] leaves. Inflorescences few- or many-flowered terminal and/or axillary, sometimes raceme-like, thyrses [or simple to compound dichasia] with minute caducous bracts. Flowers small, greenish [white], hypogynous or perigynous, [bisexual or] unisexual (the plants dioecious), with articulate pedicels. Calyx campanulate, 5-lobed, the lobes imbricate, persistent in fruit. Petals 5, inserted under the margin of the disc. Stamens 5, inserted on [or under] the margin of the disc, abortive and sterile in ♀ flowers; filaments subulate [or linear]; anthers introrse, ovate [oblong] in outline, apiculate, cordate at base, dorsifixed and usually versatile, laterally or introrsely dehiscent by 2 longitudinal slits. Nectariferous disc membranaceous and cupuliform [or fleshy and flat], shallowly 5-lobed [or entire]. Gynoecium usually 3(4)-carpellate, rudimentary in ♂ flowers; stigma usually 3(4)-lobed [the lobes sometimes bifurcate]; style short; ovary superior, usually incompletely [completely] 3-locular, with axile placentae at the very base; ovules 2 [1] in each locule, ascendent, usually with a cup-shaped aril at base, the nucellus thin. Fruit a small orange to yellow subglobular [to cylindric] leathery capsule, about 1 cm. in diameter, tipped by the persistent style, usually incompletely 3-locular, 3-valved; locules 2(1)-seeded. Seed ascendent, ellipsoidal, usually ± plano-convex, obtuse at base, attenuate toward the apex, inclosed in a fleshy crimson aril open at apex; seed coat thin, brown, leathery; endosperm copious; embryo broad-spatulate; radicle inferior. LECTOTYPE SPECIES: *C. scandens* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 492, 493. 1913. (Name from Greek, *kelastros*, the ancient name of an evergreen tree, presumably *Phillyrea latifolia* L., Oleaceae, applied by Linnaeus to this genus.)

A primarily tropical genus of about 30 (or more) species, widely distributed in eastern Asia, Malaysia, Australia, Oceania, Madagascar, and continental America. Hou (1955) established subg. CELASTRUS (flowers unisexual, ovary locules 2-ovulate, fruits usually 3–6-seeded), with 23 species in the Old World and one in eastern North America, and subg. RACEMOCELASTRUS Hou (flowers bisexual, ovary locules 1-ovulate, fruits usually 1-seeded) ranging from central Mexico to South America (seven species).

The primarily northeastern American *Celastrus scandens*, climbing or false or American bittersweet, waxwork, $2n = 46$, with ovate to elliptic leaves and terminal inflorescences, occurs in thickets, woods (most frequently in stands of young trees), fence-rows, and along streams, usually in rich soil, from southern Quebec west to southern Manitoba, south to Oklahoma and central Texas, Arkansas, Tennessee, northern Alabama, and western North Carolina, although it is scattered and rare in the states of our area.[4] This species "is related to the eastern Asiatic center of

[4] Fernald (Gray's Man. Bot. ed. 8. 984. 1950), Small (Man. SE. Fl. 818. 1933), and some other authors, include also Georgia and Louisiana, or Mississippi (Small), in the range of *Celastrus scandens*. The occurrence of *C. scandens* in Louisiana is doubtful, since C. A. Brown (Louisiana trees and shrubs, 1945, p. 169) says, "Reported

dispersion rather than to the one in Central America" (Hou, 1955, p. 224). The Asiatic *C. orbiculatus* Thunb., $2n = 46$, with suborbicular to obovate leaves and axillary inflorescences, often grown as an ornamental, has become naturalized in at least the Northeastern States, south to Virginia. Recently it has also been noted by Hoffman as naturalized in Tennessee in the Great Smoky Mountains National Park.

Little is recorded regarding floral biology in the genus. Hymenopterous insects, especially bees, seem to be the main pollinators, although wind may also be involved (cf. Wyman, pp. 84, 85).

Apomixis (adventitious embryony from the inner integument), and perhaps "false polyembryony" (supposed on the basis of the occasional occurrence of two nucelli in an ovule), and parthenocarpy have been recorded in *Celastrus scandens* (Andersson). Birds are considered to be the seed dispersing agents. Seeds in *C. scandens* which mature in the fall seem to have a long dormancy period and should be stratified to accelerate germination. Vegetative reproduction by suckers seems to be common.

Chromosome numbers are known only for the two species mentioned here. The artificial hybrid *C. scandens* × *orbiculatus* is less vigorous than the parents, sparingly fertile, and smaller fruited than either parent. The occurrence of natural hybrids between some species in eastern Asia seems probable (Hou, 1955 p. 225).

The flowers are regarded by Berkeley as perigynous, the cup-shaped disc (free from the ovary) being interpreted as a floral tube.

The genus is closely related to the pantropical *Maytenus* Molina.

*Celastrus scandens, C. orbiculatus*, and a few other species are grown as ornamentals. All are strangling vines, and our species may cause distinctive injuries to the stem and branches of young trees (Lutz). Leaves of *C. scandens* are said to be poisonous to horses.

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Under family references see ANDERSSON (pp. 1–40), BERKELEY, HOU (pp. 233–238), LOESENER (1942, pp. 131–134), and METZ (pp. 340, 341).

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DILLINGHAM, F. T. The staff-tree, *Celastrus scandens*, as a former food supply

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from West Feliciana Parish by R. S. Cocks. There are no specimens of this in the Tulane herbarium. The material so labeled is the star vine, *Schizandra coccinea* Michx. The author has searched for this plant in the state but never found it." No herbarium material of this species from Mississippi and Georgia nor documented published records from these states have been available to me; therefore the occurrence of *C. scandens* in these states cannot be confirmed at present. Suspecting that the herbarium specimen of this species collected in the southern part of Columbia County, Florida, (*Hitchcock 267*) may represent *Schisandra glabra* (Brickell) Rehd., rather than *Celastrus scandens*, I am reluctant to include Florida in the range of the species until Hitchcock's specimen is located and checked and/or the species is re-collected in northern Florida.

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WYMAN, D. Fruiting habits of certain ornamental plants. Arnoldia **10:** 81–85. 1950. [*Celastrus*, 84, 85.]

3. **Maytenus** Molina, Sagg. Stor. Nat. Chili 177. 1782; emend. Bosc, Nouv. Dict. Hist. Nat. **14:** 211. 1803.

Evergreen, usually glabrous shrubs or small trees. Leaves alternate, fleshy-coriaceous [or membranaceous to coriaceous], entire [or toothed], short-petiolate; stipules minute, caducous [or wanting]. Inflorescences compact fascicles or flowers solitary [or in dichasial cymes, short thyrses, or racemes] in leaf- or more rarely in cataphyll-axils. Flowers short-pediceled, small, usually hypogynous, [bisexual or] unisexual by abortion, the plants monoecious or dioecious. Sepals (4) 5, small, connate at least at base, persistent. Petals (4) 5, greenish white or white [or yellow, or red], longer than the sepals, spreading. Stamens (4) 5, inserted on or under the margin of the disc, shorter than the petals, reduced and sterile in ♀ flowers; filaments subulate, distinct; anthers ovate-suborbicular in outline, half as long as the filaments, introrse. Nectariferous disc conspicuous, fleshy, flattish and (4)5-angular [to -lobed] in ♂, annular and fused with the base of the ovary in ♀ flowers. Gynoecium [2]3(–5)-carpellate, rudi-

mentary in ♂ flowers; stigma [2]3(–5)-lobed; style very short or wanting; ovary superior, ± immersed in and fused at least at base with the disc, short-conical, slightly 3(–5)-angular, incompletely [or completely] 3(–5)-locular, with axile placentae at base; ovules 1 [2] in each locule, ascendent, apotropous. Fruit an ellipsoidal or obovoid, usually slightly 3(–5)-angular, coriaceous, red (our species) capsule 8–12 mm. long, 1[–3]-locular, 3(–5)-valvate, (1)3(–5)[–6]-seeded. Seed ascendent, ovoid-ellipsoidal, 3–5 mm. long, covered entirely [or partly] by a fleshy scarlet [white] aril; seed coat crustaceous [coriaceous]; endosperm fleshy [or wanting]; embryo with the radicle inferior. TYPE SPECIES: *M. boaria* Molina. (Derived from *maytén*, the vernacular Chilean name of the type species.)

A pantropical genus of over 200 species. In accordance with a broad concept of the genus (cf. Hou), *Maytenus* is here delimited to include *Gymnosporia* (Wight & Arn.) Benth. & Hook. and *Moya* Griseb. The subgeneric classification of the inclusive genus has not yet been established, but all the American species (except four formerly included in *Moya*) belong to *Maytenus* proper, i.e., to subg. MAYTENUS. The primarily South American sect. TRICERMA (Liebm.) Loes., including seven species, is represented in our area by *Maytenus phyllanthoides* Benth., a shrub or small tree with rather small fleshy-leathery obovate to oblanceolate leaves, elsewhere known from Mexico (Baja California and Sonora to Yucatán and Puebla), Central America (?), coastal southwestern Texas, and Cuba. It occurs in the hammocks and coastal sand dunes on the Florida Keys, northward along the coasts of peninsular Florida to Levy County (Seahorse Key) on the west, and Palm Beach County on the east.

Little is known concerning the floral biology, pollination, seed germination, and other biological features of either our species or the genus in general. Birds seem to be dispersal agents. The only chromosome number reported is $2n = 80$ for *Maytenus Vitis-Idaea* Griseb. (Argentina, Uruguay, Paraguay, and Bolivia), a close relative of *M. phyllanthoides*.

The genus differs from *Celastrus* mainly in the nonscandent habit, the flowers largely in compact axillary fascicles or solitary, and the ovary ± immersed in and fused at least at base with the disc.

REFERENCES:

Under family references see HOU (pp. 238–243), LOESENER (1942, pp. 134–146), METZ (pp. 341, 342), SARGENT (pp. 676, 677), and WEST & ARNOLD (p. 126).

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Subfam. CASSINOIDEAE Loes.

Tribe CASSINEAE

4. **Crossopetalum** P. Browne, Civ. Nat. Hist. Jamaica 145. *pl. 17. fig. 1.* 1756.

Usually evergreen shrubs or small trees. Leaves opposite, rarely some [or all] alternate or whorled, chartaceous to thin-coriaceous, entire, or more often serrulate to serrulate-crenate or spinose-dentate [rarely rudimentary and caducous], short-petiolate; stipules minute, subulate or rudimentary (punctiform). Inflorescences short [rarely rather ample] axillary, simple or compound (once to four times forked) dichasial cymes. Flowers very small, hypogynous, bisexual, 2-bracteolate at the base of the slender pedicels. Sepals 4, connate into a 4-lobed calyx, persistent. Petals red or purplish [greenish or white], spreading to reflexed. Stamens 4, distinct, inserted between the lobes of the disc; filaments subulate, short; anthers small, suborbicular in outline, introrsely or laterally dehiscent. Nectariferous disc + annular to low-cupuliform, usually ± 4-lobed. Gynoecium [2]4-carpellate; stigmas [2] 4, narrow, spreading; style usually short [rarely wanting]; ovary superior, [2]4-locular; ovule 1 in each locule, ascendent from the base of the axile placenta, apotropous. Fruit a red drupe, usually obliquely obovoid, 3–6 mm. long, excentrically apiculate by the persistent style, 1(2)-seeded; mesocarp fleshy, thin; endocarp bony or crustaceous. Seed small, obovoid, exarillate; seed coat membranaceous, pale brown, obsoletely minutely reticulate, with a branched raphe; endosperm fleshy, usually copious [sparse to wanting]; embryo spatulate; cotyledons ovate or suborbicular-ovate; radicle inferior. (*Rhacoma* L. Syst. Nat. ed. 10. 2: 896. 1759, nom. illeg.; a proposal to conserve this almost universally used name has been rejected. Including *Myginda* Jacq.) TYPE SPECIES: *Rhacoma Crossopetalum* L. = *Crossopetalum Rhacoma* Crantz. (Name from Greek, *crossos*, fringe, and *petalon*, petal, i.e., referring to the fimbriate petals of the type species.)

A tropical American genus of nearly 25 species, best represented in the West Indies and Central America, a few species in northern South America, and two in the southernmost part of our area.

The West Indian *Crossopetalum Rhacoma* (*C. austrinum* J. R. Gardn., *Rhacoma Crossopetalum* L.), a shrub or small tree with relatively small obovate or elliptic, usually serrulate-crenate leaves, occurs in hammocks and on coastal sand dunes on the Florida Keys and in southernmost peninsular Florida (Dade County). *Crossopetalum ilicifolium* (Poir.) Kuntze (*C. floridanum* J. R. Gardn., *Myginda ilicifolia* Poir., *Rhacoma ilicifolia* (Poir.) Trel.), a prostrate shrub with coriaceous spiny-toothed leaves 10–15(20) mm. long, occurs in pinelands in the same areas of subtropical Florida [5] and beyond in the Bahamas and Hispaniola.

[5] A recent record (Hayes) of this species from a locality in the Coastal Plain of eastern North Carolina is apparently based either on an introduced plant or on a

The genus appears to be closely related to *Cassine* L. (*Elaeodendron* Jacq. f.) and more remotely allied to *Gyminda* Sargent.

REFERENCES:

Under family references see LOESENER (1942, pp. 183–185), METZ (pp. 380, 381), URBAN (pp. 69–79), and WEST & ARNOLD (p. 127).

HAYES, D. W. Two remarkable range extensions (*Rhabdadenia corallicola* and *Rhacoma ilicifolia*). Castanea **11**: 61, 62. 1946. [Both collected by W. A. Dayton in acid soil at Blackland Branch Station near Wenona, Washington Co., N.C.]

5. **Gyminda** Sargent, Garden Forest **4**: 4. 1891.

Dioecious glabrous evergreen shrubs or small trees. Leaves opposite, thin-coriaceous, entire or crenulate [serrate], short-petiolate; stipules minute, membranaceous, lanceolate to linear-lanceolate, caducous. Inflorescences short, simple to compound (1–4 times forked), peduncled axillary cymes. Flowers very small, hypogynous, unisexual by abortion, minutely 2-bracteolate just below the calyx, sessile. Sepals 4, nearly distinct, persistent. Petals 4, white, longer than the sepals, spreading or reflexed. Stamens 4, alternipetalous, distinct, inserted between the lobes of the disc, wanting in ♀ flowers; filaments subulate; anthers suborbicular in outline, laterally-introrsely dehiscent. Disc fleshy, 4-lobed in ♂, crenulate, adnate to the base of ovary in ♀ flowers. Gynoecium *2*(3)-carpellate, rudimentary in ♂ flowers; stigmata 2, ample, commissural, peltate, nearly semiorbicular, sessile, persistent on fruit; ovary superior, *2*(3)-locular; ovule 1 in each locule, pendulous from the top of axile placenta, anatropous, apotropous. Fruit an ellipsoidal to obovoid drupe, 6–8 mm. long, black or dark blue, crowned with persistent stigmata, *2*(3)-locular (1 locule often rudimentary), (1)*2*(3)-seeded; mesocarp fleshy, thin; stone bony. Seed ellipsoidal or cylindric-ellipsoidal, exarillate; seed coat membranaceous, finely foveolate-reticulate; endosperm fleshy, thin; embryo spatulate, the cotyledons ovate or oblong, the radicle subcylindrical, superior. TYPE SPECIES: *G. latifolia* (Sw.) Urb. (Name an anagram of *Myginda*, to which this plant had been referred.)

A genus of two or three (?) species of subtropical North America, the West Indies, and Central America south to Costa Rica. The West Indian *Gyminda latifolia* (*G. Grisebachii* Sarg.), false-boxwood, occurs in hammocks on the Florida Keys. Records of this species from Mexico may perhaps refer to the closely related Central American *G. Tonduzii* Loes. The latter seems to be rather variable in the shape and size of leaves, and some specimens (forms?) with smaller and more rounded leaves (than those usually seen) can easily be confused with *G. latifolia*, as often also are sterile (and rarely flowering) specimens of *Crossopetalum Rhacoma*.

The genus is most closely related to and perhaps congeneric with the

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mistake in labeling. At present there hardly is a reason to regard *C. ilicifolium* as either native to or naturalized in North Carolina.

monotypic Jamaican *Tetrasiphon* Urb., which differs from *Gyminda* only in its four-carpellate gynoecium, four oblong-linear stigmata, and fibrous innermost layers of mesocarp. The genus also shows a relationship to *Maurocenia* Mill., *Cassine* L. (*Elaeodendron* Jacq. f.), and *Crossopetalum*. It differs from *Cassine* and *Crossopetalum* in its pendulous ovules and, if combined with either of these, would be an anomalous group with regard to this characteristic.

REFERENCES:

Under family references see LOESENER (1942, p. 182), METZ (pp. 377, 378), SARGENT (pp. 678, 679), URBAN (pp. 80–83), and WEST & ARNOLD (p. 127).

SARGENT, C. S., *Gyminda*. Silva N. Am. **2**: 13, 14. *pl. 54*. 1891.

6. **Schaefferia** Jacquin, Enum. Syst. Pl. Ins. Carib. 10. 1760.

Dioecious, evergreen, usually glabrous shrubs or trees. Leaves alternate, ± coriaceous, entire [rarely toothed], short-petiolate; stipules subulate or rudimentary. Flowers small, hypogynous, unisexual by abortion, manifestly pediceled, in axillary few-flowered fascicles or solitary. Sepals 4, nearly distinct, persistent. Petals 4, much longer than the sepals, yellowish or whitish, spreading or reflexed, cochleate-imbricate. Stamens 4, hypogynous, shorter than the petals, wanting in ♀ flowers; filaments subulate; anthers broad-elliptic-subquadrangular, dorsifixed near base, hardly versatile, introrsely dehiscent. Nectariferous disc indistinct and adnate to the base of ovary in ♀, wanting in ♂ flowers. Gynoecium 2-carpellate, rudimentary in ♂ flowers; stigmata 2, commissural, large, usually 2-lobed to -fid, spreading or reflexed; style very short, stoutish, or wanting; ovary superior, sessile, 2-locular; ovule 1 (2) in each locule, ascendent from the base of the axile placenta, apotropous. Fruit a small, scarlet, subglobular, thin-fleshed drupe, nearly 5–6 mm. in diameter, indistinctly 2-lobed, crowned by the persistent style and or bases of stigmata; stones (pyrenes, "nutlets") 2, or 1 by abortion, somewhat obovoid, plano-convex, with rough ± tuberculate cartilaginous endocarp. Seed ellipsoidal or ovoid, plano-convex, exarillate; seed coat membranaceous, smooth, brownish; endosperm copious; embryo spatulate, the radicle inferior. TYPE SPECIES: *S. frutescens* Jacq. (Named for Jacob Christian Schaeffer, 1718–1790, distinguished German naturalist and mycologist.)

A tropical American genus of nine species, ranging from Peru, northern Argentina, and Uruguay, northward to the West Indies, southernmost Florida, western Texas, and northern Mexico; one species in the subtropical part of our area.

*Schaefferia frutescens*, Florida boxwood, yellow-wood, distributed in the West Indies, Venezuela and Colombia, and northward in Central America to southern Mexico, occurs in hammocks on the Florida Keys and in extreme southeastern peninsular Florida. According to Sargent (1891),

the ripe fruits possess an acrid disagreeable flavor but are greedily eaten by many birds. *Schaefferia cuneifolia* Gray, a small shrub, occurs in the arid region of western Texas and northern Mexico.

Loesener (1942) assumed *Schaefferia* to be closely related to *Crossopetalum* but to approach Aquifoliaceae in its discless staminate flowers. The genus also resembles the latter family in the general structure of the fruits (convergent evolution?).

REFERENCES:

Under family references see LOESENER (1942, p. 189), METZ (pp. 383, 384), SARGENT (pp. 689, 690), URBAN (pp. 84–87), and WEST & ARNOLD (p. 128).

RECORD, S. J., & G. A. GARRAT. Boxwoods. VIII. Florida boxwood of the family Celastraceae. Yale School Forestry Bull. **14**: 75–77. 1925. [*S. frutescens*, wood anatomy.]

SARGENT, C. S. *Schaefferia*. Silva N. Am. **2**: 15–18. *pl. 55*. 1891.

## HIPPOCRATEACEAE A. L. de Jussieu, Ann. Mus. Hist. Nat. Paris **18**: 486, 1811, "Hippocraticeae," nom. cons.

(HIPPOCRATEA FAMILY)

Woody vines with slender, scandent branches [or shrubs, or slender trees], often with ± anomalous wood, frequently with latex ducts in all organs [or only in the axis], differing from Celastraceae mainly in the almost exclusively opposite leaves; extrastaminal nectariferous disc; usually 3-merous androecium; usually extrorse anthers often dehiscing by transversally confluent slits; occurrence of pollen tetrads in some taxa; usually 6–8[2–20]-ovulate locules; pleurotropous ovules; and frequent occurrence of peculiar, usually 3-locular, deeply 3-parted capsules with large, dorsiventrally flattened, radially divergent segments containing endospermless seeds winged from the base. TYPE GENUS: *Hippocratea* L.

A pantropical family of about 21 genera with nearly 400 species. It is centered and almost equally represented (with regard to the genera) in America and Africa, with a few taxa in Asia and Australasia. Only *Hippocratea* is represented in the subtropical part of our area.

No data on floral biology or anatomy are available; those on embryology pertain to six genera. Pollen has been studied in 44 species of 14 genera (mostly African, three Afro-American, one pantropical). Chromosome counts for ten species in seven genera (two Afro-American, one pantropical) invariably have been $2n = 28$ in the genera with berry- or drupelike fruits (e.g., *Salacia* L., *Salacighia* Loes., of subfam. Salacioideae Hallé), and $2n = 56$ in the genera with capsular fruits (e.g., *Campylostemona* Welw.; *Hippocratea, sensu stricto*; and *Loeseneriella* A. C. Sm., of subfam. Hippocrateoideae). Polyploidy apparently has been of importance in the evolutionary development of the family.

The peculiar shape of the capsules of the members of subfam. Hippocrateoideae is due to a disproportionate growth of the ovary after fertiliza-

tion. While the size of the axis of the ovary and the lower placentiferous parts of the locules remains almost unchanged during the process of fruit development, the tips of the locules expand greatly, forming segments [or lobes] up to 50–100 times longer than the length of the central placentiferous part of the mature fruit. Since the basal placentiferous parts of the locules (including the funicles) remain permanently united with the persistent fruit axis after dehiscence of the expanded locular tips, such a fruit is to be classified as a somewhat modified capsule, rather than as an apocarpous or schizocarpous fruit.

The taxonomy of the Hippocrateaceae has been based primarily on the gross morphology of the reproductive organs, on some characters of the inflorescence, and, in some cases, on palynological data. Differences in evaluation of these characters have resulted in varying numbers of recognized genera, e.g., nine (including *Campylostemon* and *Cheiloclinium* Miers [placed in Celastraceae] in Loesener, 1942) or 21 (Smith, 1940, 1941, 1945; Wilczek, 1960; Hallé, 1962). The generic concepts of the last three authors are accepted here, but it is likely that additional data on floral anatomy, embryology, cytology, etc., will create a basis for a considerable reduction in the number of genera.

This very natural group is closely related to and sometimes included in (most recently by Blakelock) the Celastraceae, which name is conserved over Hippocrateaceae when the two are united. A relationship to Siphonodontaceae and Stackhousiaceae is also presumed.

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HALLÉ, N. Monographie des Hippocratéacées d'Afrique Occidentale. Mém. Inst. Franç. Afr. Noire **64:** 1–245. 1962. [Fifteen genera: 9 African, 3 Afro-American, 2 Afro-Asiatic, 1 pantropical.]

LOESENER, T. Hippocrateaceae. Nat. Pflanzenfam. III. **5:** 222–230. 1896.

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1. **Hippocratea** Linnaeus, Sp. Pl. 2: 1191. 1753; Gen. Pl. ed. 5. 498. 1754.

Latex-bearing vines with scandent, usually opposite branches. Leaves opposite, membranaceous to subcoriaceous, petiolate, persistent; stipules minute, subulate, caducous. Inflorescences axillary, corymbose-paniculate, dichotomously branched, peduncled cymes, usually with 1 or 2 short, few-flowered branchlets in each dichotomy, with minute bracts and bractlets. Flowers small, regular, hypogynous, bisexual, pediceled. Sepals 5, connate at least at base, imbricate [or valvate]. Petals 5, distinct, yellowish [or whitish], thickish, much longer than the sepals, spreading, with a transverse tomentulose band below the apex within [or tomentulose except at the base], narrowly imbricate [or valvate]. Disc extrastaminal, conspicuous, fleshy, annular-pulvinate, subcylindrical or truncate-conical [or ± cup shaped], puberulent [or glabrous] without. Stamens 3, suberect, spreading, or reflexed; filaments strap shaped, dilated toward and often contiguous at base, often adnate to the upper margin of the disc; anthers basifixed, oblate-spheroidal, dehiscing by horizontal (transverse) extrorse-apical slits; pollen 3- or 4-porate, in compound tetrads (polyads) of 16 grains. Gynoecium syncarpous, 3-carpellate; stigma small, punctiform or

inconspicuously 3-lobed; style short, subulate; ovary 3-locular, 3-lobed, sessile, completely immersed in and fused with the disc, at least at the base; ovules usually 6[–8] in a locule, 2-ranked, ± ascendent, anatropous. Fruit a 3-locular, deeply 3-parted capsule, with divergent, dorsiventrally (vertically) flattened segments (the greatly expanded tips of the locules), each dehiscing loculicidally along an inconspicuous median suture; pericarp membranaceous to thin-coriaceous. Seeds 5 or 6 in each capsule segment, each with a basal wing jointed at the base with a fleshy, nearly obdeltoid funicle, the embryoniferous apical portion of seed coriaceous, flattened, the wing membranaceous, with a marginal and a submedian longitudinal nerve; endosperm wanting; embryo straight; cotyledons large, distinct, fleshy, flat; radicle minute, inferior. TYPE SPECIES: *H. volubilis* L. (Named for Hippocrates, 460–377 B.C., eminent Greek physician, "Father of Medicine.")

A genus of one American and two African species. The tropical American *Hippocratea volubilis* (*H. scandens* Jacq., *H. ovata* Lam.) occurs in hammocks and mangrove swamps in southernmost peninsular Florida (Dade, Monroe, Collier, and Lee counties) and on the Florida Keys, in the West Indies, and from central Mexico, south to Peru, Bolivia, northern Argentina (Misiones), Paraguay, and southern Brazil. Within its extensive range the species exhibits numerous variations on which many supposedly distinct species have been based (see A.C. Smith, 1940, for a complete synonymy).

The genus has often been delimited in a broad sense (cf. Loesener, 1942; Blakelock, 1958) to include all the species (over 100) of Hippocrateaceae with very similar capsular fruits and winged seeds (except *Campylostemon* Welw. and *Tristemonanthus* Loes., both with introrse stamens). In 1940, however, A. C. Smith restricted *Hippocratea* to the type species. Recently two African species (*H. myriantha* Oliver and *H. Vignei* Hoyle) have been included in *Hippocratea, sensu stricto* (see Hallé, 1962). Thus delimited, *Hippocratea* differs from closely related segregate genera (e.g., *Pristimera* Miers, *Prionistemma* Miers, *Elachyptera* A. C. Sm., *Reissantia* Hallé, *Loeseneriella* A. C. Sm.) both in some floral characters (e.g., petals tomentulose within in *Hippocratea*, configuration of the disc) and in the compound pollen tetrads and the presence of latex in all parts of the plant (a questionable generic character in this family). In general, the characters distinguishing *Hippocratea, sensu stricto*, from the closely related genera are of such a nature that they may eventually be regarded as subgeneric, in view of the rather uniform anatomy of vegetative organs and the gross morphology of fruits and seeds (cf. Aceraceae).

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AQUIFOLIACEAE Bartling, Ord. Nat. Pl. 228, 376. 1830, nom. cons.

(Holly Family)

Shrubs or trees, differing from Celastraceae mainly in the almost exclusively alternate leaves, the usually sympetalous rotate corolla, the absence of a nectariferous disc (but cf. *Schaefferia*); the almost exclusively one-ovulate locules, the always pendulous one-integumented ovules, and the minute "rudimentary" embryo in the vicinity of the micropyle. Type genus: *Aquifolium* Mill., nom. illeg. = *Ilex* L.

A family of three genera: the primarily pantropical polytypic *Ilex*; the monotypic *Nemopanthus* Raf., endemic in northeastern North America; and the tropical *Phelline* Labill. (ten species), endemic in New Caledonia. Only *Ilex* is represented in our area; *Nemopanthus mucronatus* (L.) Trel. occurs from Newfoundland to Minnesota, southward to northern Illinois, Indiana, Ohio, and upland West Virginia and Virginia.

Aquifoliaceae exhibit a number of primitive characters (e.g., the minute "rudimentary" embryo; the exclusively scalariform perforation plates in vessels), as well as specialized features (e.g., the often sympetalous corolla; the absence of a nectariferous disc, apparently due to abortion; the solitary, one-integumented ovules). A relationship to Celastraceae (especially to subfam. Cassinoideae) has generally been assumed, and the evidence from gross morphology of flowers and fruits, wood anatomy, and embryology seems to support this view. Pollen morphology does not furnish positive indications in favor of such a relationship (Erdtman, p. 55), but it should be noted that only two genera of subfam. Cassinoideae, the group apparently closest to Aquifoliaceae, have been investigated.

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1. **Ilex** Linnaeus, Sp. Pl. 1: 125. 1753; Gen. Pl. ed. 5. 60. 1754.

Dioecious evergreen, or more rarely deciduous, shrubs or trees of acid, often wet soils. Leaves alternate [exceptionally opposite], simple, thick-coriaceous to membranaceous, entire, crenate, serrate, or spiny toothed, petioled; stipules minute, usually caducous, more rarely persistent. Inflorescences axillary to leaves or bracts on either long- or short-shoots, single or fascicled 1- to many-flowered dichasial cymes, sometimes umbel-like and/or panicled [or racemes], or flowers solitary or in fascicles. Flowers small, hypogynous, unisexual by abortion. Sepals 4–9, connate in a 4–9-lobed (to -parted) calyx, imbricate, persistent. Petals 4–9, [rarely distinct] usually connate into a sympetalous rotate corolla, usually white, greenish-white or -yellow [rarely pink, red, or lavender], imbricate. Stamens 4–9, alternipetalous, usually adnate at base to the short corolla tube, more rarely distinct, nearly as long as the petals in ♂, abortive and sterile in ♀ flowers; filaments subulate or straplike; anthers ovoid to ellipsoidal, introrse, dorsifixed, not versatile, dehiscing by 2 lateral longitudinal slits, 2-locular at anthesis; pollen 3-colp(oroid)ate, spheroidal to subprolate (or prolate?), medium sized, coarsely and densely granular on the surface. Gynoecium syncarpous, 4–9[–22]-carpellate, rudimentary in ♂ flowers; stigma mostly sessile or subsessile, large, capitate or discoid [or columnar], mostly ± lobed, persistent in fruit; style wanting or very short; ovary superior, 4–9[–22]-locular; ovules 1 (occasionally 2) in each locule, pendulous from the top of the axile placenta, anatropous, apotropous, 1-integumented, with a thickish nucellus; funiculus often with a prominent protuberance on the entire adaxial surface. Fruit a subglobular to ellipsoidal berry-like drupe, usually red, more rarely dark purple to black, occasionally yellow to whitish, containing [2]4–9[–22] unilocular stones (pyrenes, "nutlets") shaped like citrus-fruit segments [exceptionally a single 4-locular stone]; exocarp chartaceous; mesocarp fleshy or sometimes ± coriaceous because of stone cells interspersed in its outer layers; endocarp bony or woody, rarely coriaceous, the back (and sides) of stones either completely smooth and even, or more often longitudinally striate and/or ridged and grooved, sometimes sparsely irregularly reticulate. Seed solitary (occasionally 2) in a stone, pendulous; seed coat membranaceous; endosperm copious, fleshy; embryo minute, obversely heart shaped, situated near the micropyle. (Including *Prinos* L.) LECTOTYPE SPECIES: *I. Aquifolium* L.; see N. L. Britton, N. Am. Trees. 621. 1908. (Classical Latin name of the Mediterranean holly oak, *Quercus Ilex* L., applied by Linnaeus to this genus.) — HOLLY.

A primarily pantropical genus of 300–400 species, centered in eastern Asia (southern and southwestern China and Indochina) and South America (Brazil), with one species in tropical Africa, one in Australia, and one in Europe; about 14 species (all represented with us) occur in eastern North America. Since the genus is currently being studied by several workers and its classification is still in flux, the relatively simple but at least partly unnatural one of Asa Gray is followed here (Gray, Man. eds. 1–5. 1848–1869; Fernald, Gray's Man. Bot. ed. 8. 980–982. 1950).[6]

Subgenus ILEX (subg. *Euilex* Loes., subg. *Aquifolium* (DC.) Gray). Leaves persistent, thin- to thick-coriaceous, sometimes spiny toothed; short-shoots lacking; carpellate flowers usually 4-merous; drupes red; stones (pyrenes) longitudinally (2)3–5-striate (sometimes faintly so) and/or ridged and grooved or irregularly thinly reticulated on the back. The largest and most widely distributed subgenus, it is represented with us by *Ilex opaca* Ait. var. *opaca*, American holly, $2n = 36$, and var. *arenicola* (Ashe) Ashe (*I. arenicola* Ashe, *I. cumulicola* Small), scrub holly; *I. vomitoria* Ait. var. *vomitoria*, yaupon or cassena, $2n = 40$; *I. Cassine* L., dahoon holly; and *I. myrtifolia* Walt. The principal taxonomic problems revolve around the status of *I. opaca* var. *arenicola*, of the sand scrub of peninsular Florida, which has been treated as a distinct species (correctly named *I. arenicola*), and that of the relationships of *I. Cassine* and *I. myrtifolia*, which have sometimes been regarded as varieties of a single species. *Ilex vomitoria* is notable for the caffeine content of the leaves, a concentrated infusion of which was used by the Indians of the Coastal Plain in a stimulating and emetic "black drink." The species occurs disjunctly in Chiapas and Vera Cruz, Mexico, as the pubescent var. *chiapensis* Sharp. *Ilex* × *attenuata* Ashe, a presumed natural hybrid between *I. Cassine* and *I. opaca*, has been recorded from northwestern Florida and both Carolinas.

Subgenus PRINOS (L.) Gray, Man. Bot. No. U. S. ed. 2. 264. 1856 (*Prinos* L.; including subg. *Euilex* Loes. sect. *Cassinoides* Loes. Nat. Pflanzenfam. Nachtr. 218. 1897, in part). LECTOTYPE SPECIES: *Prinos verticillata* L. = *Ilex verticillata* (L.) Gray; see Hitchcock & Greene, Int. Bot. Congr. Cambridge 1930. Nomencl. Propos. Brit. Bot. 147. 1929. Leaves deciduous or persistent; carpellate flowers (4)6–8(9)-merous; stones smooth and even, rarely indistinctly 1-striate on the back. Largely a temperate eastern Asiatic-North American group of about 12 species, extending with one or two species into the West Indies and Central America. Five species, comprising three morphological groups, occur in our area. *Ilex verticillata* (L.) Gray, winterberry, black alder, or fever bush, $2n = 36$, and *I. laevigata* (Pursh) Gray, smooth winterberry, are deciduous shrubs or small trees with red (rarely yellow) drupes. By contrast, *I. glabra* (L.) Gray, inkberry, gallberry, or bitter gallberry;

[6] Following Gray's classification, Fernald mistook his subgeneric names for those of sections (cf. Brizicky, Jour. Arnold Arb. **44**: 62, footnote 3. 1963). For much more elaborate classifications of *Ilex*, see Loesener (1901, 1942) and Hu (1949–1950; and in Dengler, 1957, pp. 31–64).

*I. coriacea* (Pursh) Chapm., large or sweet gallberry; and the West Indian *I. Krugiana* Loes., which reaches Dade County, Florida, are all black-fruited evergreen species placed by Loesener in subg. ILEX. The last species differs, however, from the former two in its epunctate leaves, four-merous flowers, and fascicled inflorescences and seems to represent a distinct, primarily South American group (sect. *Microdontae* Loes.). Although the three groups have many similarities in the morphology of flowers and fruits, their relationships are highly questionable. *Ilex glabra* and *I. coriacea* are similar in many characteristics and are often confused, although they appear to be distinct species. *Ilex glabra* is regarded by foresters as an undesirable plant in pinewoods, but it seems to be an important source of honey in the Gulf region.

Subgenus PRINOIDES (DC.) Gray, Man. Bot. No. U. S. 276. 1848 (subg. *Prinos* sect. *Prinoides* (DC.) Gray ex Loes. Nat. Pflanzenfam. Nachtr. 221. 1897). LECTOTYPE SPECIES: *Ilex prinoides* Ait. = *I. decidua* Walt.). Leaves deciduous, membranaceous to subcoriaceous, often crowded on short spurs (short-shoots); carpellate flowers 4–5(6)-merous, often crowded on short-shoots; drupes red (occasionally yellow); stones as in subg. ILEX. A temperate eastern Asiatic-North American group of about 12 species, five or six in our area. The subgenus seems to be closely related to and is often included in subg. PRINOS (cf. deciduous, red-fruited species). Our species include *Ilex montana* Torr. & Gray var. *montana* (*I. monticola* Gray), mountain winterberry or mountain holly, $2n = 40$, and the pubescent-leaved var. *mollis* (Gray) Britton (including *I. Beadlei* Ashe ex Kearney); *I. decidua* Walt. var. *decidua*, possum-haw, $2n = 40$, and a small-leaved Florida variant, var. *Curtissii* Fern. (*I. Curtissii* (Fern.) Small); *I. ambigua* (Michx.) Torr., Carolina holly; *I. longipes* Chapm. (including *I. collina* E. J. Alex., fide Edwin), Georgia holly; and the very rare *I. Amelanchier* M. A. Curtis (*I. dubia* (G. Don) BSP., 1888; not Weber, 1851, pl. fossil.), sarvis holly, of sandy swamps from Louisiana to Georgia and southeastern Virginia. *Ilex Cuthbertii* Small apparently should be included in *I. decidua*, while *I. Buswellii* Small, found in hammocks along the Caloosahatchee River in southwestern Florida, may perhaps be a small-leaved form of *I. ambigua*. *Ilex longipes* is remarkable for its fruits with pedicels 1.2–2.2 cm. long.

It is notable that several eastern North American species have counterparts in eastern Asia, e.g., *I. montana–I. Tsoi* Merr. & Chun; *I. decidua–I. aculeolata* Nakai; *I. longipes–I. asprella* (Hook. & Arn.) Chapm.; *I. glabra–I. yunnanensis* Franch.; *I. verticillata–I. serrata* Thunb. var. *Sieboldii* (Miq.) Rehder (Hu, 1949, p. 255).

It seems likely that diversification of inflorescence types in *Ilex* has generally been due to the reduction and simplification of an original ample compound dichasial cyme (or cymes) along several divergent or convergent lines, rather than to the elaboration of a simple dichasium. Solitary or fascicled single-flowered inflorescences and solitary or fascicled flowers seem to be the final products of lines of reduction. Within a species, the carpellate inflorescences usually are somewhat more reduced than the

staminate ones (sexual dimorphism), e.g., fascicled simple staminate dichasia, but fascicled single-flowered carpellate inflorescences in *I. Krugiana*; solitary 3–7-flowered dichasial staminate cymes, but solitary single-flowered carpellate inflorescences in *I. glabra*; fascicled staminate flowers, but solitary carpellate flowers in *I. coriacea*. No correlation between the types of inflorescence and the fruit (pyrene) characters has yet been demonstrated.

Since the species of the genus usually are dioecious, although the occasional occurrence of bisexual flowers has been recorded in *I. Aquifolium*, cross-pollination and -fertilization are the rule. Insects, especially bees, have been recorded as pollinators, but wind apparently also is a factor in pollination in some species. The nectar is said to be excreted from small papillose swellings found at the base or near the middle of the petals on their adaxial (upper) surface (Loesener, 1942, p. 45).

Although a single axile ovule in each locule is typical, the occasional occurrence of two-ovulate locules has been recorded. Herr (1959) demonstrated that the two-ovulate condition is due to the presence of a second parietal rudimentary ovule ("parietal protuberance") in the ovary locule which maintains a potentiality to develop. Also, the "funicular protuberance," considered by Herr to be a partially suppressed nonfunctional ovule, can sometimes develop into a regular ovule.

Chromosome counts made in ten species ($2n = 36, 40$) possibly indicate polyploidy, with the basic numbers supposedly $x = 9, 10$. *Ilex* × *attenuata* is the only wild interspecific hybrid known in eastern North America; the occurrence of many forms intermediate between the species of *Ilex* in eastern Asia, especially in south and southwest China (Hu, 1949, p. 254) may suggest more extensive hybridization in that region. Many artificial and or natural hybrids of garden and nursery origin are known at present. Most are within subg. ILEX and involve *I. Aquifolium* as one of the parents, but a few are in subg. PRINOS (sensu Gray), e.g., *I. glabra* × *serrata*, *I. crenata* × *glabra*. The established hybrid *I. Aquifolium* × *yunnanensis*, and the suspected *I. chinensis* × *glabra* are intersubgeneric (according to the classification used here) or intersectional (according to that of Hu).

Birds are considered to be the seed dispersing agents. Parthenocarpy seems to be common in *I. laevigata* and *I. cornuta* Lindl., less so in *I. vomitoria*, but apparently is of wider distribution, since a natural tendency to parthenocarpy has also been found in several other species (e.g., *I. Aquifolium*, *I. Cassine*, *I. myrtifolia*). The rudimentary embryo of *Ilex* undergoes maturation after dispersal but prior to germination (Herr. 1962, p. 32), which usually occurs in nature from one to three years after dispersal. The percentage of germination is low, and as a rule, the seeds are very difficult to germinate.

Many foreign and indigenous species are grown as ornamentals (e.g., the European *I. Aquifolium* with its numerous varieties and hybrids, the eastern Asiatic *I. cornuta* and *I. crenata*, the domestic *I. opaca*). The berried branches of *I. Aquifolium* and *I. opaca* are in great demand for Christmas decoration, and those of *I. laevigata* and *I. verticillata* are

sometimes sold for this purpose. Leaves of the South American *I. paraguariensis* St. Hil. (and possibly of a few other closely related species) yield the maté or Paraguay tea which is much used in South America. The wood of some arborescent species is valued for lathe work, engraving, and cabinet-making.

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# THE GENERA OF LYTHRACEAE IN THE SOUTHEASTERN UNITED STATES [1]

SHIRLEY A. GRAHAM

LYTHRACEAE Jaume St.-Hilaire, Expos. Fam. **2:** 175. 1805, "Lythrariae," nom. cons.

(LOOSESTRIFE FAMILY)

Herbs or shrubs [rarely small trees], with quadrangulate or terete stems. Leaves opposite, seldom alternate or whorled, simple, entire, exstipulate. Flowers regular or irregular, axillary or in terminal racemes or spikes, sometimes dimorphic or trimorphic with regard to style and stamen length, bisexual, [3]4–6-merous, with perianth and stamens perigynous, the flowers rarely cleistogamous; bracteoles 2, opposite on the pedicel, rarely none. Floral tube campanulate to tubular, persistent, often conspicuously nerved; calyx lobes 4–6, alternating with 3–5 deltoid appendages, or the appendages wanting. Petals 0–6, distinct, crumpled, deciduous [rarely persistent], inserted on the inner surface of the floral tube between the calyx lobes. Stamens as many as or twice as many as the petals [or more numerous], often alternately unequal, inserted on the inner surface of the floral tube below the petals, included to exserted; anthers versatile [rarely basifixed], introrse, 2-locular, longitudinally dehiscent. Gynoecium syncarpous, often surrounded at the base by a hypogynous disc, or in irregular flowers the disc on the upper (adaxial) side only; stigma capitate, rarely bilobed; style filiform; ovary superior, free in the floral tube, 2–4[–6]-locular, the septa complete or reduced; placentation axile [rarely parietal]; ovules anatropous and epitropous, with 2 integuments. Fruit a membranaceous [or leathery] capsule inclosed by the persistent floral tube, septicidally or loculicidally dehiscent or indehiscent, splitting irregularly. Seeds 3 to many, minute or up to ca. 4 mm. long, pyramidal, ovoid, or discoid, sometimes slightly winged, with

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Reed C. Rollins and Carroll E. Wood, Jr. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39:** 296–346. 1958). The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in the descriptions in brackets applies to species outside this area, and references marked by an asterisk have not been seen by the author.

The aid of Dr. Wood and the observations and suggestions of Drs. H. E. Ahles, R. K. Godfrey, D. B. Ward, and C. A. Brown are gratefully acknowledged. Dr. R. B. Channell kindly supplied living material of *Cuphea* for study.

little or no endosperm; embryo straight with a short radicle, the cotyledons flat [rarely convolute], often auriculate-cordate. Embryo sac development of the normal (Polygonum) type (rarely intermediate between Polygonum and Oenothera type); endosperm development of the nuclear type. (Salicariae Juss., 1789.) TYPE GENUS: *Lythrum* L.

A family of about 24 genera and 450 species, most abundant in the New World tropics and subtropics, but present in temperate to tropical areas of Europe, Asia, Africa, and Australia; six genera represented in our area.

Koehne (1903) divided the family into two tribes based on the condition of the septa in the ovary. In tribe Lythreae the septa are interrupted or split above the placenta, which is then discontinuous with the style; in Nesaeeae Koehne the septa are complete and the placenta is continuous with the style. This character is variable and difficult to ascertain in many specimens. If tribal divisions are to be used at all, a firmer basis for their delimitation is needed.

Similarities in anatomy and embryology closely link the Lythraceae with the Myrtaceae, Onagraceae, Punicaceae, and Sonneratiaceae (see Mauritzon, 1939). The Lythraceae are distinguished from these families by the superior ovary which is free in the floral tube. The family is characterized anatomically by intraxylary phloem which forms bicollateral bundles in the leaves.

Unique, spirally grooved, inverted hairs are found in the epidermal layer of the seed coat in several genera (e.g., *Cuphea*, *Peplis*, and some species of *Lythrum*). Upon contact with water, the hairs emerge through the outer wall of an epidermal cell and slowly uncoil to a length of two or three millimeters. The hairs are slightly mucilaginous and may serve in dispersal by attaching the seed to passing objects.

Heteromorphism is widespread in the family. *Lythrum*, *Decodon*, and *Nesaea* have species with trimorphic flowers, and species with dimorphic flowers are known in *Lythrum*, *Rotala*, *Pemphis*, and *Nesaea*. Cleistogamous flowers have been reported in *Ammannia* and are thought to occur in the apetalous species of *Rotala*, *Peplis*, and *Nesaea*.

Fossil remains of the Lythraceae are known from the Eocene through the Pleistocene. At least six genera of fossil seeds belonging to the Lythraceae have been described. All are well suited to aquatic dispersal by means of winglike expansions of the seed coat and/or buoyant spongy tissue on the outer seed coat. The aquatic or semiaquatic habit of many Lythraceae is undoubtedly an ancient characteristic, still present, but less prevalent in modern species.

Two genera, *Lawsonia* and *Lagerstroemia*, are cultivated in warm-temperate and tropical regions of the world. *Lawsonia inermis* L., native to northeastern Africa, is the henna of commerce, yielding an orange-red dye which has been used for centuries in the Near and Far East for coloring the hair, fingernails, and soles of the feet. The leaves contain hydroxynaphthaquinone which reacts directly with the keratin of human hair and skin to form the bright pigment.

The crape-myrtle, *Lagerstroemia indica* L., $2n = 48, 50$, a native of Asia, is a very popular shrub or tree widely cultivated throughout our southern states. It is showy in bloom, producing great numbers of magenta flowers. A number of horticultural varieties bearing purple, pink, or white flowers are planted. The trees are long lived and may persist where planted long after dwellings have disappeared. For this reason, they may appear to be naturalized but are usually only remnants of cultivation and not true escapes. One possible exception is the presence of several young plants in the sparsely inhabited sand-hill country of Berkeley County, South Carolina (*H. E. Ahles 52982*, NCU). Collectors of this species should note the circumstances under which the plants are growing and record any evidence of reproduction from seed.

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## KEY TO THE GENERA OF LYTHRACEAE

General characters: *Leaves entire, mostly opposite; floral tube campanulate to cylindrical, persistent; ovary superior, free in the floral tube; petals crumpled; fruit capsular; seeds without endosperm, the embryo straight.*

A. Floral tube campanulate to globose, about as long as wide.
  B. Plant woody, perennial, over 1 m. tall.
    C. Flowers in axillary dichasia; stamens 8–10; shrubs of shallow water. ..... 1. *Decodon.*
    C. Flowers in terminal panicles; stamens numerous, more than 10; terrestrial trees or shrubs. ..... [*Lagerstroemia.*]
  B. Plant herbaceous, annual, generally less than 50 cm. tall.
    D. Appendages in the sinuses of the calyx lobes present; capsule dehiscent; flowers 1 to many in the axils of leaves; petals 4 (rarely 0).
      E. Middle and upper leaves attenuate at base; capsule dehiscing septicidally, the outer wall of capsule finely and densely striate; flowers solitary in the axils of leaves. ..... 2. *Rotala.*
      E. Middle and upper leaves cordate to auriculate at base; capsule dehiscing irregularly, the outer wall of the capsule smooth, not striate; flowers (1–)3 to many in the axils of leaves. ..... 3. *Ammannia.*
    D. Appendages in the sinuses of the calyx lobes none; capsule indehiscent; flowers solitary in the axils of leaves; petals 0. 4. *Peplis.*
A. Floral tube cylindrical, elongate, about twice as long as wide.
  F. Flowers regular; floral tube entire in fruit; capsule dehiscing septicidally from the apex, the placenta included; seeds numerous, mostly more than 20. ..... 5. *Lythrum.*
  F. Flowers irregular; floral tube and capsule splitting longitudinally along the upper (adaxial) side in fruit, the placenta then exserted; seeds 3–20. ..... 6. *Cuphea.*

### 1. Decodon J. F. Gmelin, Linn. Syst. Nat. ed. 13. 2(1): 677. 1791.

Short-lived glabrous or pubescent perennial shrubs or tall herbs of marshy habitats, spreading by means of arching branches rooting at the tips; stems terete to 6-angled, the submerged portions thickened by spongy aerenchyma. Leaves membranaceous to leathery, decussate or verticillate, lanceolate, shortly petiolate, the base and apex acute. Inflorescence of 1–3 shortly pedunculate axillary dichasia at a node, the peduncles partly fused with the petiole. Flowers regular, 4- or 5-merous, trimorphic;

bracteoles 2, ovate to linear, opposite, at the base of the pedicel, early deciduous. Floral tube campanulate, greenish, inconspicuously nerved; calyx lobes 4 or 5(–7), the apex acuminate; appendages narrowly triangular, thickened, mostly twice the length of (rarely equal to) the calyx lobes. Petals 4 or 5(–7), rose-purple, deciduous, about twice the length of the floral tube. Stamens 8–10, deciduous; filaments of 3 possible lengths, two of the three lengths occurring in any one flower and alternating in a single whorl; anthers orbicular in outline. Gynoecium sessile, the disc wanting; stigma capitate; style thin, included to exserted, of 3 possible lengths; ovary 3(4)-locular, the septa complete. Fruit a loculicidally dehiscent capsule. Seeds ca. 20–30, small, inverted-pyramidal with rounded edges, an oval germination valve covered by a spongy epidermal layer present on the adaxial side. TYPE SPECIES: *D. verticillatus* (L.) Ell. (Name from Greek, *deca*, ten, and *odous*, tooth, in reference to the five sepals and five appendages of the floral tube.) — SWAMP LOOSESTRIFE, WATER-OLEANDER, WATER-WILLOW.

A monotypic genus now occurring only in the eastern United States from Louisiana to Florida and north to Minnesota and central Maine. The glabrous var. *laevigatus* Torr. & Gray has been recognized in the northern part of the range. In the Mio-Pliocene the genus was represented by at least two other species from western Europe and central Russia. Fossil seeds of these suggest they were very closely related, but not identical, to the extant *Decodon verticillatus*. Silicified fruit remains from the Eocene of India may represent either *Decodon* or an extinct genus similar to it.

Extensive aerenchyma is produced in concentric layers on submerged stems. The tissue is composed of large thin-walled parenchyma supported by radial columns of cells and by additional strands of elongated cells which obliquely cross several layers to strengthen the tissue. The meristem which produces aerenchyma develops in a narrow zone of parenchyma between the phloem fibers and sieve tube area. Some species of *Ammannia* and *Lythrum* in aquatic situations also develop aerenchyma, but to a lesser degree than in *Decodon*.

Endlicher subordinated *Decodon* to a section of *Nesaea*, but most subsequent authors have regarded it as distinct.

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2. **Rotala** Linnaeus, Mant. Pl. Alt. 175. 1771.

Annual [rarely perennial], glabrous herbs of aquatic or marshy habitats. Leaves membranaceous, decussate, verticillate, or alternate, linear to oblanceolate [to ovate], attenuate to the base, sessile to short petioled. Flowers regular, solitary and axillary [or in terminal spikes], [3]4–6-merous, [seldom dimorphic,] sessile, with 2 opposite bracteoles at the base of the floral tube. Floral tube campanulate to globose or urceolate, 2.5–5 mm. long, greenish; calyx lobes 4[–6], the apex acute to acuminate; appendages shorter than to exceeding the lobes [or wanting]. Petals [0 or] 4[–6], white or pink, small, scarcely exceeding the calyx lobes, deciduous [rarely persistent]. Stamens 4[–6], included [to exserted]. Gynoecium without a disc at the proximal end; stigma capitate; style very short or wanting; ovary incompletely 3- or 4[–6]-locular, the upper portion of each septum ± incomplete. Fruit a membranaceous, septicidally dehiscent capsule with dense, transverse striations on the outer wall, [2-]3- or 4-valved. Seeds many, minute, ovoid in outline, plano-convex. TYPE SPECIES: *R. verticillaris* L. (Name from Latin, *rota*, wheel, in allusion to the whorled leaves of the type species.) — TOOTH-CUP.

A genus of about 45 species, best represented in Asia and Africa. Of the three North American species, only *Rotala ramosior* (L.) Koehne, $2n = 32$, is present in our area, occurring in all the Southeastern States. The more robust plants occurring inland from the Atlantic Coastal Plain have been recognized as var. *interior* Fern. & Grisc. The species closely resembles *Ammannia* in general habit and was originally described in that genus. Bentham and Hooker considered *Rotala* synonymous with *Ammannia*, but the close resemblance to *Ammannia* is found only in *R. ramosior*; the genera can be distinguished easily on the basis of at least three characters. *Rotala* has solitary axillary flowers, a septicidally dehiscent capsule, and the outer wall of the capsule densely striate, a character present in no other genus of the Lythraceae. In *Ammannia* the flowers occur in axillary cymes, the capsule dehisces irregularly, and the outer wall of the capsule is smooth.

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3. **Ammannia** Linnaeus, Sp. Pl. 1: 119. 1753; Gen. Pl. ed. 5. 55. 1754.

Annual glabrous herbs of aquatic or marshy habitats. Leaves membranaceous, decussate, linear to lanceolate or oblanceolate, sessile, the base cordate to auriculate, rarely attenuate. Flowers regular, 4(5)-merous,

never heteromorphic, in sessile or pedunculate axillary cymes, (1–)3–15 flowers at a node; bracteoles 2, linear, opposite, at the base of the floral tube. Floral tube campanulate to urceolate, becoming globose in fruit, 1.5–6 mm. long, greenish to rose colored, 8-nerved with 4 nerves especially prominent at anthesis; calyx lobes 4 (5), short and broad; appendages thick, shorter than to equaling the calyx lobes [or wanting]. Petals 0–4, small, pink [white], early deciduous. Stamens 4(–8), included to exserted. Gynoecium without a disc at the base; stigma capitate; style thin, longer than the ovary and exserted, or thick, shorter than the ovary and included; ovary incompletely 2–4(5)-locular, the upper portion of the septa ± incomplete. Fruit a membranaceous, irregularly dehiscent capsule, with the outer wall smooth, not striate. Seeds many, minute, ovoid. LECTOTYPE SPECIES: *A. latifolia* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. **2**: 577. 1913. (Named in honor of Paul Ammann, 1634–1691, a German botanist from Leipzig, not Johan Ammann; see Linnaeus, Crit. Bot. 91. 1737.)

A genus of world-wide occurrence, with about 20 species; represented in the southeastern United States by two to four species. *Ammannia coccinea* Rottb. is found throughout the eastern United States, in the western coastal states, and in Mexico, Central America, the Caribbean region, and northern South America. In Mississippi and elsewhere outside our area (e.g., Oklahoma, Missouri, and Indiana), intermediates occur between this and *A. auriculata* Willd., which is generally found west of the Mississippi River. *Ammannia auriculata* differs from *A. coccinea* mainly in having more densely clustered, smaller, long-pedicellate flowers. A third species, *A. teres* Raf., of swamps or fresh to brackish tidal marshes, ranges from New Jersey to Florida, Mississippi, and Texas. In southern Florida it is replaced by *A. latifolia* L., which extends southward through the Antilles into northern South America. The two are distinguished only by the lack of petals in *A. latifolia* and should probably be considered variants of a single species. Cleistogamous flowers have been reported in *A. latifolia*. A re-evaluation of specific limits in the genus is needed.

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4. **Peplis** Linnaeus, Sp. Pl. 1: 332. 1753; Gen. Pl. ed. 5. 154. 1754.

Delicate annual herbs growing along lake margins or submerged in shallow water. Leaves membranaceous, opposite or alternate, sessile, narrowly linear or oblanceolate, the base acute to obtuse. Flowers regular,

4[–6]-merous, solitary, axillary on short pedicels or sessile; bracteoles 0 [or 2, opposite on the pedicel]. Floral tube broadly campanulate [to globose], 2–3 mm. long; calyx lobes 4[–6], the appendages wanting [or long-subulate]. Petals 0 [or 6, but early deciduous]. Stamens (2?) 4[–6], included. Gynoecium without a disc at the base; stigma capitate or slightly bilobed; style very short or wanting; ovary incompletely 2-locular, appearing 1-locular by reduction of the septum. Fruit a membranaceous, indehiscent capsule, splitting irregularly. Seeds many, small, dorsiventrally flattened, spathulate, the distal end slightly enlarged and curved. (Including *Didiplis* Raf.) TYPE SPECIES: *P. Portula* L. (Ancient Greek name applied by Dioscorides to *Euphorbia Peplis* and by Pliny to "porcillaca or purslain," *Portulaca oleracea*.) — WATER-PURSLANE.

A European genus of eight species; represented in the United States by the endemic *Peplis diandra* Nutt. ex DC., which ranges from Florida to eastern Texas, northward to Minnesota, and to North Carolina. This species displays a terrestrial form having cuneate-lanceolate leaves and a short style, and an aquatic form which generally has longer, narrower, linear leaves, shorter internodes, and no style. The specific epithet *diandra* is perhaps misleading, being based on an atypical plant with only two, rather than the normal four, stamens.

The separation of *Peplis diandra* by some authors as *Didiplis diandra* (DC.) Wood has been made on the basis of its four-merous, rather than six-merous, flowers and the lack of appendages on the floral tube. In view of the numerous other shared characters, e.g., irregularly splitting capsules with many seeds, campanulate floral tube, general plant habit, there seems to be no reason for retaining *Didiplis* as distinct from *Peplis*. Koehne considered *Didiplis* synonymous with *Peplis* but circumscribed subg. DIDIPLIS for this one species.

No insect visitors have been reported for the genus. The most widespread European species, *Peplis Portula* L., $2n = 10$, is known to be self-pollinated, and the floral morphology suggests that this is probably the rule for the other species. The stigma is short and in a position to receive pollen from the introrse anthers lying above it in the floral tube, while insect-attracting petals and nectaries are wanting. Cleistogamy is suspected in the apetalous species.

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5. **Lythrum** Linnaeus, Sp. Pl. 1: 446. 1753; Gen. Pl. ed. 5. 205. 1754.

Annual or perennial herbs or shrubs of moist, often brackish habitats. Leaves membranaceous, decussate, alternate [or verticillate], ovate to

linear [or obovate], sessile or shortly petiolate, the base attenuate to cordate. Flowers regular [or slightly irregular], (4–)6-merous, sometimes heteromorphic with 2 [3] floral forms, the flowers axillary [or in terminal spikes or racemes], 1 or 2 [to several] sessile or shortly pedicellate flowers at a node; bracteoles [0] 2, on the pedicel, linear, opposite. Floral tube cylindrical, greenish, 8–12-nerved, 4–8 mm. long; calyx lobes (4–)6, the apex acute to acuminate, the appendages narrowly triangular, shorter than to exceeding the calyx lobes. Petals (4–)6 [rarely 0], rose-purple or white, deciduous. Stamens (4–)6[–12] in 1 [2] whorls, inserted deep in the floral tube, included to exserted; filaments in heteromorphic forms of 2 [3] lengths. Gynoecium sessile or stipitate, with or without a hypogynous disc at the proximal end; stigma capitate; style thin, included to exserted, in heteromorphic forms of 2 [3] lengths; ovary 2-locular, the septum ± incomplete. Fruit a membranaceous [rarely leathery] capsule, dehiscing septicidally or septifragally. Seeds [8 to] many, small, ovoid in outline. LECTOTYPE SPECIES: *L. Salicaria* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 580. 1913. (Name from Greek, *lythron*, gore or blood; thought to refer to the purple color of the petals.) — LOOSESTRIFE.

A genus of about 30 species, with its greatest development in North America (ca. 16 species), but also occurring in Europe, Asia, Africa, and Australia. The North American species are badly in need of revision. Past treatments have depended heavily on variable characters of the leaf for delimitation of species. Hybridization among species in different parts of their range is suspected but has not been studied. Understanding of the breeding patterns and morphological variation seems necessary for a more satisfactory treatment of this group.

The genus is represented in our area by six weakly defined species of sect. EUHYSSOPIFOLIA Koehne (plants grayish or bluish-green, calyces mostly tubular, flowers 4–6-merous, petals present). The most common and widespread indigenous *Lythrum* in the eastern United States is *L. lanceolatum* Ell., characterized by appendages exceeding the sepals and alternate, linear to elliptic leaves with tapering bases. Within its range is *L. Curtissii* Fern., reportedly endemic to southwestern Georgia and adjacent Gadsden County, Florida. This species, with slightly smaller flowers, larger stem leaves, and smaller branch leaves than *L. lanceolatum*, probably represents a local variant of *L. lanceolatum*. *Lythrum lineare* L., named for its linear, strictly opposite leaves, is restricted to brackish marshes on or near the coast from New Jersey to Florida, and west along the gulf coast to eastern Texas. Specific lines separating *L. alatum* Pursh, $2n = 10$, *L. dacotanum* Nieuw., and *L. flagellare* Shuttl. ex Chapm. are very tenuous. Misinterpretation of *L. alatum* has increased difficulties in recognizing species within this group (see Shinners).

Several species in North America (including *Lythrum lanceolatum*, *L. lineare*, and *L. alatum*) have two floral forms, an individual having either flowers with long styles and short stamens or short styles with long

stamens. The plants are generally self-sterile and outbreeding. The most successful crosses occur between stamens and styles of corresponding lengths. Pollination is accomplished by insects. The most detailed studies on dimorphic flowers have been conducted on the genus *Primula* (Primulaceae). The dimorphic *Lythra* have not been investigated.

The occurrence of plants having three floral forms was first noted by Vaucher (1841) in *Lythrum Salicaria* L., $2n = 30, 50, 60$, a Eurasian species long naturalized in Canada and the northeastern United States and now occurring southward at least to Virginia. The first extensive account of this phenomenon was given by Darwin (1865). In this species there are three style lengths and three sets of stamens of lengths corresponding to those of the styles. Each floral form has one style length and two whorls of stamens, one whorl for each of the other two possible lengths. The forms are termed long-, mid-, or short-styled, depending on whether the style exceeds, lies between, or is shorter than the two whorls of stamens. An individual plant bears only one of the three floral forms.

Genetically, the long-styled form has been shown to be homozygous and recessive for long styles, while the short-styled form differs from long- and mid-styled by a single epistatic gene. The mid-styled flowers carry duplicate factors for "mid-" in the same linkage group, with the homozygous condition of either or both factors producing a lethal effect.

Pollen differs in color, size, and amount of stored starch in each of the three stamen lengths. The longest stamens have the largest grains, the anthers are green, and the pollen grain is filled with starch. The two shorter stamen lengths have yellow anthers and correspondingly smaller pollen containing less starch. The two kinds of pollen in each floral form carry identical hereditary factors for the inheritance of trimorphism. In like manner, the stigmatic papillae vary in length with the length of the style, being longest on the longest style.

The flowers are slightly irregular, with the stigma and anthers bent upward toward the open side of the flower. Insects of several different orders visit the species. They are able to pass only along the open side of the flower to reach the nectar at its base, and, in moving toward the nectaries, their underside brushes both the upturned stigma and the anthers. The pollen is transported on the ventral side of the insect mainly in three places, corresponding to the position of the three stamen lengths, and is consequently transferred to styles of those lengths, effecting cross-pollination.

Crosses occurring between style and stamens of corresponding length are very fertile and are termed "legitimate" unions; conversely, those between style and stamens of unequal length (including self-pollinated flowers) are generally unsuccessful and are termed "illegitimate" unions. Exceptions are the successful crosses obtained between mid-styled plants pollinated by long stamens of the short-styled form and short stamens of the long-styled form. It is probable that pollen from more than one stamen length is dusted onto a style, but studies indicate that unidentified chemical

growth inhibitors present in the style prevent the pollen of illegitimate unions from competing with that of legitimate unions.

Products of most illegitimate crosses are highly sterile, often dwarfed, and rarely persist. Seedlings of mid-styled illegitimate crosses are, however, more hardy and fertile than other illegitimate unions. Darwin found that although the mid-styled form produced seed by illegitimate as well as legitimate unions, the stamens of that form were less fertile than were those corresponding stamens of the other two forms, suggesting that in the mid-styled form there is a tendency toward functional dioecism. All three forms are believed to have been derived from a single homomorphic, self-compatible form. A semihomomorphic form has been reported in which the style and one whorl of stamens are the same length, being intermediate in position between long- and mid-styled forms. It has been suggested that heterostyly is an unstable state in *Lythrum Salicaria*, the presence of an intermediate form and the variable degrees of self-compatibility evidenced by the three floral types tending to support this conclusion. Trimorphism has been reported for only four other genera: *Nesaea* and *Decodon*, of the Lythraceae; *Oxalis*; and a single monocotyledonous genus, *Pontederia*.

Fossil flowers of *Lythrum* have been found in the Lower Pliocene of Japan (see Miki). This determination is based on the flower's being four-sepalate, a rare condition in modern species. Miki also found fossils of *Trapa* and *Hemitrapa* Miki (an extinct genus) and, on the basis of a comparative study, concluded that *Trapa* was derived from *Lythrum* through *Hemitrapa*. Other writers consider Trapaceae closely related to, and perhaps derived from, Onagraceae.

Chromosome numbers of $2n = 10$, 20, 30, 50, and 60 have been reported for the genus, but only one count has been published for the indigenous American species.

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6. **Cuphea** P. Browne, Civ. Nat. Hist. Jamaica 216. 1756.

Herbaceous or woody annuals or short-lived perennials, mostly with viscid, glandular hairs on stem, leaves, and flowers. Leaves membranaceous [or leathery], decussate or verticillate [rarely alternate], ovate to lanceolate, elliptic or linear, sessile or petiolate. Flowers irregular, 6-merous, homomorphic, sessile or pedicellate, 1–3 at a node: when alternate on the stem one flower at each node interaxillary, the others, if present, axillary; when opposite or verticillate on the stem all flowers interaxillary and often internodal; bracteoles 2, opposite, on the pedicel. Floral tube cylindrical, 4–10[–25] mm. long, green or purple, distinctly 12-nerved, the base gibbous or distinctly spurred, the spur curving downward toward [or upward away from] the pedicel; calyx lobes 6, deltoid, acute to acuminate [rarely apiculate] at apex, equal in size or the upper (adaxial) one larger than the others; appendages shorter than [to exceeding] the length of the calyx lobes. Petals 6 [4, 2, or 0], pale to deep purple, equal in size or the upper (adaxial) 2 or the lower (abaxial) 4 largest, early deciduous [rarely persistent]. Stamens (5–)11(–12), included to exserted, alternately unequal, the filaments often covered with dense hairs, the 2 upper (adaxial) stamens inserted deeper in the calyx tube than the others; pollen triangular or orbicular in outline in polar view, [2]3-colporate, the exine striate. Gynoecium with a disc at the base on the upper side only and free from the side of the ovary; stigma capitate, seldom bilobed; style included or exserted; ovary incompletely 2-locular, appearing 1-locular by reduction of the septum to 2 thin threads, the lower (abaxial) locule smaller, sometimes sterile. Fruit a membranaceous, loculicidally dehiscent capsule, splitting longitudinally the length of the adaxial wall of the ovary, the upper (adaxial) side of the persistent floral tube also splitting, the placenta projecting up and out of the capsule and floral tube. Seeds 3–20[–numerous], orbicular to ovoid in outline, dorsiventrally flattened [rarely not flattened], the surface pebbled, dark brown [mottled green and brown, or light brown], often narrowly margined; cotyledons flattened, cordate to auriculate; radicle short. (*Parsonsia* P. Br.) TYPE SPECIES: *C. decandra* Ait. (*C. ciliata* (Sw.) Koehne, 1881, not *C. ciliata* Ruiz & Pav., 1798). (Name from Greek, *kuphos*, hump, referring to the gibbous or spurred floral tube.)

A genus of 200–250 species, in 13 sections, mostly restricted to the American tropics and subtropics; represented in our area by four species in three sections. The sections are very weakly delimited, and discovery of new species and accumulation of knowledge of variability in the species have further lessened their validity. The entire genus is in need of revision, with emphasis on a more natural arrangement of the species.

The most common species of our area is the annual *Cuphea viscosissima* Jacq. (*C. petiolata* (L.) Koehne, 1881, not *C. petiolata* Pohl ex Koehne, 1877), tarweed or blue waxweed, an endemic to the United States, which ranges from northern Alabama and Georgia and western North and South

Carolina, to central Arkansas, and northward to easternmost Kansas and Massachusetts. Reportedly a bad weed in pastures, old fields and gardens, it is avoided by livestock because of its dense, sticky, glandular hairs. It is most closely related to species of western and central Mexico. A second indigenous species, *C. aspera* Chapm. (*Parsonsia lythroides* Small), with opposite flowers, whorled leaves, pale-purple petals, and tuberous roots, is known only from the immediate vicinity of Port St. Joe, Florida. It is most closely related to *C. hyssopoides* St.-Hil., of Brazil.

The South American *Cuphea glutinosa* Cham. & Schlecht. was first collected in the United States in 1884, in Vermilion Parish, Louisiana, a general area to which it has remained restricted. The petals are characteristically very early deciduous. The presence of *C. carthagenensis* (Jacq.) Macbr. (*C. balsamona* Cham. & Schlecht.) along our coast from Louisiana to North Carolina often has been overlooked. It has been confused with the common *C. viscosissima*, in spite of its distinct geographical range and very different morphology (floral tube green *vs.* purple and green, 4.5–6 mm. *vs.* 8–10 mm. long, petals equal in size *vs.* upper (adaxial) petals largest, and stamens deeply *vs.* shallowly inserted in the tube). The species is native to South America but has spread as far west as the Fiji and Philippine islands and is undoubtedly a relatively recent introduction to the United States. Most early collections are misidentified as *C. viscosissima*. A showy-flowered Mexican species, *C. procumbens* Cav., has been reported from the Blue Ridge, North Carolina, and Andover and Springfield, Massachusetts. These plants were most likely garden escapes which would not have persisted. There is no evidence that the species is established in the eastern United States today.

The genus is morphologically the most highly specialized in the family. It is well adapted to insect and hummingbird pollination by virtue of the long, irregular floral tube, the loss of a stamen in the honey entrance, and the introrsely directed anthers. Glandular-viscid bristles on the floral tube and stems discourage crawling insects from entering the flower, while a disc at the base of the flower narrows the passage to the nectar secreted by the walls of the spur, excluding all but long-tongued insects. Most species are apparently self-compatible but require an insect vector to accomplish pollination. The seeds emerge from the capsule and floral tube while green and remain on the placenta, exposed to the air, for a ripening period.

The interaxillary position of the flowers of *Cuphea* is unique in the family. In the alternate-flowered species, a vegetative bud is present in the axil of one leaf and a floral bud in the axil of the other. The vegetative bud may produce a flowering branch (sometimes highly reduced), or remain suppressed; the floral bud produces a single flower, the pedicel of which traverses and is fused with the internode above, the flower emerging just below or at the node above, between the leaves. In opposite-flowered species, both flowers at the node are interaxillary.

Pollen morphology differs among some species and in these cases provides a useful taxonomic character. One fossil pollen grain of *Cuphea* is known from the Miocene of Alabama. It is three-colporate but does not

belong to any of the species present in the United States today. According to Erdtman, *Cuphea* is isolated from the other genera of the family on the basis of pollen morphology.

Embryologically, *Cuphea* is quite distinct from *Ammannia*, *Nesaea*, *Rotala*, *Peplis*, and *Lythrum*. Its relationship to other genera in the family has not been investigated. Chromosome numbers of $2n = 12$, 16, 18, 20, 24, 32, 36, 72, and ca. 84 have been found in the genus (Graham, unpublished). No counts have been reported for the species in our area.

A few species are cultivated; the best known are *Cuphea platycentra* Lem. (*C. ignea* A. DC.) and *C. procumbens* Cav., commonly called cigar or firecracker plants, after the long, purple or red floral tube.

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# POLYEMBRYONY IN EUONYMUS (CELASTRACEAE) [1]

GEORGE K. BRIZICKY

POLYEMBRYONY, the production of two or more embryos within a seed, is rather widely, although sporadically, distributed among the spermatophytes. Although less common than in the gymnosperms, polyembryony in the angiosperms is much more diverse in respect to the origin and mode of development of embryos. In the angiosperms, embryos may be derived from an egg cell (rarely from two or more "egg cells") and/or synergids and/or antipodals within a single reduced or unreduced embryo sac of an ovule, either following or without fertilization; from a fertilized egg cell through the cleavage of the zygote or the proembryo (cleavage polyembryony); or directly from the cells of the nucellus or the inner integument of an ovule (adventitious embryony) (Ernst, pp. 436–438; Lebègue, pp. 333–336). Although polyembryonate species or populations usually show a predominance of one type of polyembryony, there also are those (e.g., *Allium odorum* L.) which may produce seeds with embryos derived in several different ways.

Of all the types of polyembryony those involving apomixis (either gametophytic [diplo- or apospory, parthenogenesis, or apogamety] or somatic [adventitious embryony]) are of special interest because of the effects of apomixis on the groups in which it occurs. Apomixis makes possible the survival of well-adapted but sexually sterile genotypes, permits the building up of large populations of genetically similar individuals for rapid colonization of newly available habitats, and limits the genetic variability of those plants which have adopted this mode of reproduction (Stebbins, 1950, pp. 414–416). Although a rather restrictive factor in evolution, apomixis is important in the increase of polymorphism and geographic distribution of the genera in which it occurs. The study of agamic complexes, i.e., groups of closely related apomictic and sexual species, may yield valuable information on the present and past distribution of plants and may help in the determination both of centers of origin and routes of dispersal of genera and/or their sections and of the relative ages of different floras (Stebbins, 1941, pp. 533–536).

In view of the role of apomixis in evolution and distribution, and of its bearing on taxonomy, the records of polyembryony in three species of *Euonymus* L., coupled with the great polymorphism and wide distribution

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of this genus, suggested that it would be desirable to verify Braun's record (1860) of polyembryony in *E. americanus* and to investigate the distribution of polyembryony within the genus. Since only a few special seed collections were available, the necessity of using herbarium specimens for this purpose has limited investigations to those species in which the specimens have numerous loose seeds or fruits. Consequently, only a few seeds of each species could be examined, and no strictly statistical evaluation of the results can be made. Despite this limitation, the occurrence of polyembryony in several species has been detected, and the possibility of its absence or rare occurrence in other species has been indicated.

## POLYEMBRYONATE SPECIES OF EUONYMUS

It is expedient to begin with *Euonymus latifolius* and *E. americanus*, in which polyembryony has long been known and thoroughly investigated by several authors. Other species are surveyed in alphabetical order. In citations of the material investigated by the writer the abbreviations "P" and "M" are used for polyembryonate and monoembryonate, respectively. In regard to size, embryos are described as full sized (3.5–3 mm.), subnormal (3–2 mm.), small (2–1 mm.), very small (1–0.5 mm.), minute (0.5–0.25 mm.), and very minute (under 0.25 mm.). The minute and very minute embryos usually are club shaped, subcylindrical, or subglobular, often notched at the apex; all the larger ones are distinctly differentiated into cotyledons and radicle and are similar in shape.

### Euonymus latifolius (L.) Mill.

Du Petit-Thouars (1808, p. 199), the first to record polyembryony in the genus, wrote that in *Euonymus latifolius*, although sometimes two equally developed embryos were found in the endosperm ("perispèrme") of a seed, more commonly one was much smaller than the other. Later, Grebel (1820) and Treviranus (1838) also reported the occurrence of polyembryony in this species. The main points of Grebel's observations (pp. 324, 325) were that not rarely (but neither in every capsule nor twice in a capsule) two completely developed embryos lying side by side in the endosperm cavity of a seed were observed, but more frequently one embryo of the pair was much smaller than the other, had spread cotyledons, and was leaning to the radicle of the larger embryo; and, once, three normally developed, completely mature and two minute embryos were found in the endosperm cavity. In all the cases the embryos were lying in the seed in the same position, their radicles being directed toward the hilum (micropyle). Grebel did not mention the number of seeds examined. Treviranus (p. 556, *pl. 3, fig. 40*) reported that a half of nearly a dozen seeds examined by him were two-embryonate, both embryos of each pair lying in the same position in a seed.

In 1860, Braun (pp. 157, 158, *pl. 4, figs. 1–12; pl. 5, figs. 1–4*) examined nearly fifty seeds of *E. latifolius*. Twenty-eight of these were polyem-

bryonate (twenty-four with two embryos, three with three, and one with four). All embryos in a seed were lying in the same position in respect to, but often at different distances from, the micropyle. Strasburger (1878, pp. 658, 659, *pl. 19, fig. 44*) confirmed Braun's observations and stated that most seeds examined by him were polyembryonate. He also investigated the embryology of *E. latifolius* and concluded that the egg cell, although fertilized, only rarely developed into an embryo, but the adjacent nucellar tissue penetrated into the embryo sac and gave rise to adventitious embryos. Usually, only a single cell of the nucellar tissue became the initial of an adventitious embryo, which appeared to be situated similarly to an embryo developed from a fertilized egg cell, but sometimes the development of adventitious embryos began from a large cell-complex.

Most recently Andersson (1931), investigating the embryology of the same species, reported (pp. 34, 35), "In den allermeisten Samen und Samenanlagen mit Stadien nach der Befruchtung von *Evonymus latifolius*, die ich untersucht habe, kamen zwei bis mehrere Embryonen vor. In einigen Fällen habe ich feststellen können, dass die befruchtete Eizelle stirbt. Ob das aber immer der Fall ist, weiss ich nicht. Es ist aber nicht zu verneinen, dass sogar in Samen mit einem einzigen Embryo, dieser ein Adventivembryo sein kann. Auch die Eizelle wächst. Sie teilt sich erst ziemlich spät, und dann ist es sehr schwierig zu entscheiden ob sie noch da ist oder nicht. Denn zu dieser Zeit haben sich einige Zellen des inneren Integuments vorgewölbt . . . Die Zellen geben durch ihren Plasmareichtum ihren Charakter als Initialen der Adventivembryonen zu erkennen. . . . Nicht alle Adventivembryonen werden zu derselben Zeit angelegt. . . . Es scheint mir aber, dass Embryonen auch von einem schon vorhandenen Embryo hervorsprossen können, der dann als Embryoträger fungiert. . . . Einmal habe ich eine embryoähnliche Bildung wahrgenommen, von der ich geneigt bin zu glauben, dass sie aus dem Endosperm stammt." Andersson also showed that in *Euonymus latifolius*, as in *E. europaeus* L. (*q. v.*), the nucellus disintegrates, except for a negligible residue in the chalazal region, and can not be regarded as a source of adventitious embryos. Thus, according to him, in *E. latifolius* the adventitious embryos originate from the inner integument, although he once observed an embryo possibly of endospermous origin.

## Euonymus americanus L.

Braun (1860, p. 159) investigated seeds of this species and stated that polyembryony in *Euonymus americanus* is even more common than in *E. latifolius*. Only five of twenty seeds examined by him were monoembryonate, six contained 2 embryos, four 3, three 4, and two 5. Two embryos in a seed often were subequal and full sized, the others gradually smaller, with one or two minute and easily overlooked. The relative position of the embryos in the endosperm was the same as in *E. latifolius*.

One hundred twenty-six seeds of nine collections of *Euonymus americanus* from various parts of its range were examined by me.

*Friesner 22624*, Jackson County, Indiana (GH): 5 seeds; 1 M; 4 P (three seeds with 2, and one with 3 embryos; supernumerary embryos small, minute, or very minute.

*Short 1855*, Kentucky (GH): 6 seeds; 2 M; 4 P (one with 2, two with 3, and two with 4 embryos; in all cases only one embryo in each seed full sized, the supernumerary small, minute to very minute).

*Fernald & Long 7522*, Nansemond County, Virginia (GH): 25 seeds; 1 M; 24 P (one with 10 embryos, one with 9, two with 8, four with 6, four with 5, three with 4, eight with 3, and one with 2; in one 6-embryonate seed the largest (full-sized) embryo reversed, with the radicle directed toward the chalaza; in one 6- and one 8-embryonate seed all the embryos small to very minute and lying in various positions both axially [with their radicles directed to opposite poles] and ± transversely). This specimen shows not only the highest percentage (96%) of polyembryonate seeds, but also the highest number of embryos in a seed (10), the average number being 5.

*Demaree 9576*, Montgomery County, Arkansas (GH): 5 seeds, all P (two with 2, one with 3, and two with 4 embryos; in all cases only one embryo in each seed full sized, the supernumerary small, minute to very minute).

*Demaree 16568*, Grant County, Arkansas (GH): 5 seeds; 2 M; 3 P (two with 3, and one with 4 embryos).

*R. B. Channell*, 13 Sept. 1957, Davidson County, Tennessee (preserved fruits): 50 seeds; 9 (18%) M (FIG. 1, a); 41 (82%) P (nine with 2 embryos, nine with 3, fourteen with 4, four with 5, three with 6, and two with 7; in one 3- and one 4-embryonate seed one embryo reversed [FIG. 1, b, c], with the radicle directed toward the chalaza; in a 4-embryonate seed three minute embryos situated in the micropylar region and one subnormal embryo lying across the seed [FIG. 1, d]). Four was the average number of embryos in a seed. (See also FIG. 1, e.)

*Wiegand & Manning 1908*, Henry County, Alabama (GH): 5 seeds, all P (two with 2, one with 3, and two with 5 embryos; in all the cases only one embryo in a seed full sized, the supernumerary mostly minute to very minute; in a 5-embryonate seed one minute embryo situated at the reverse pole of the endosperm cavity [opposite the micropyle] immersed in the endosperm and covered with an oil droplet). An endospermous origin of the last-mentioned embryo seems to be possible.

*Palmer 6782*, Polk County, Texas (A): 5 seeds, all P (two with 2, one with 3, and two with 4 embryos; in a 4-embryonate seed two embryos full sized).

*Kral & Godfrey 3570*, Gadsden County, Florida (GH): 20 seeds; 19 M; 1 P (with one full-sized and one small embryo).

My observations show that polyembryony in *Euonymus americanus* is rather frequent, as long ago stated by Braun (1860). Ten was the highest number of embryos found in a seed. Although all supernumerary embryos usually were found in the micropylar region in normal positions, in seven seeds one or more supernumerary embryos of a seed were situated in reverse axial and/or transverse positions (FIG. 1, b–e). In six of these seeds an integumentary origin of such embryos is assumed, but in one (*Wiegand & Manning 1908*) an endospermous origin of a reverse embryo is to be suspected. The specimen *Kral & Godfrey 3570*, perhaps representing *E. americanus* var. *angustifolius* (Pursh) A. Wood or a form close to it seems to be an exception in which polyembryony is rare.

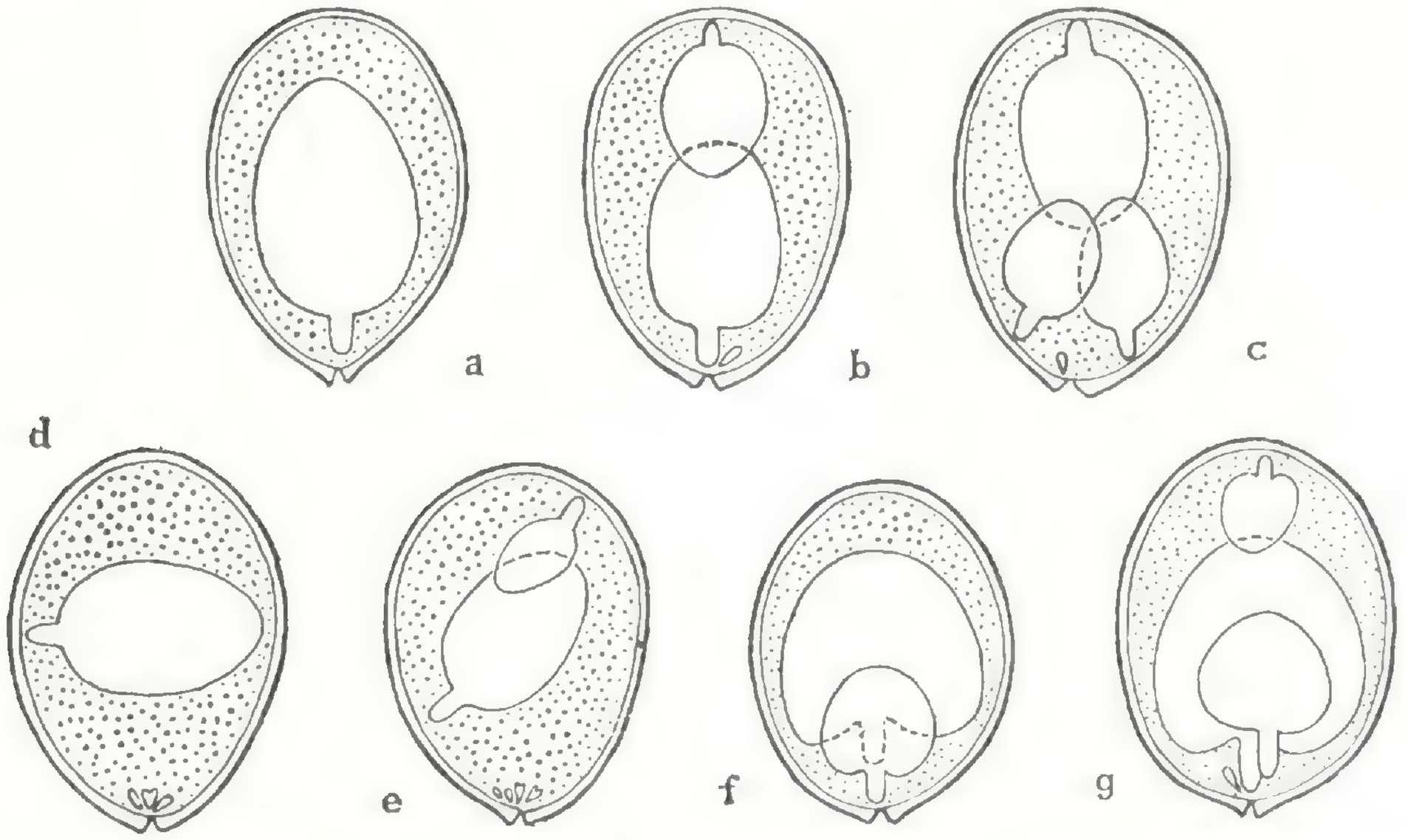


FIG. 1. Longitudinal sections of seeds of *Euonymus* to show arrangement of embryos. Drawings diagrammatic, the micropyle below, double seed coat not indicated, endosperm stippled, ca. × 5. a–e, *E. americanus* (*Channell*, Tennessee, 1957): a, monoembryonate seed; b, three-embryonate seed with embryo at chalazal end in reversed position; c, four-embryonate seed with nearly full-sized embryo in reversed position; d, four-embryonate seed with subnormal embryo horizontal, three minute ones in micropylar region; e, six-embryonate seed with one subnormal and one small embryo lying in opposite directions and four minute embryos around micropyle. f, g, *E. alatus* var. *apterus*: f, two-embryonate seed with cotyledons of smaller embryo clasping radicle of larger (*Sargent*, Japan, 16 Sept. 1892); g, four-embryonate seed with one small embryo in reversed position (Arnold Arb. no. 14543-B).

### Euonymus alatus (Thunb.) Regel var. apterus Regel

Thirteen seeds of three herbarium collections, and 200 seeds of a living cultivated plant were examined.

*W. T. Tsang 23362*, Kwangsi, China (A): 3 seeds; 1 M; 2 P (each with one full-sized and two somewhat smaller embryos).

*Wilson 354*, Western Hupeh, China (A): 10 seeds; 8 M; 2 P (each with two subequal, slightly undersized embryos).

*Sargent*, 16 Sept. 1892, Sapporo, Japan (A): 3 seeds, all P (two with 2 subequal embryos in each; one 4-embryonate seed with one embryo in a reverse position at the chalazal end of endosperm [FIG. 1, g]).

Arnold Arboretum; no. 14543-B (grown from seeds sent from Korea, by J. Jack): 200 seeds; 166 (83%) M; 34 (17%) P (twenty-eight 2-embryonate and six 3-embryonate; in all cases embryos located in the micropylar region [FIG. 1, f]).

### Euonymus dielsianus Loes.

*Stewart, Chiao, & Cheo 811*, Kweichow, China (A): 4 seeds; 1 M; 3 P (all 2-embryonate; in each of two seeds both embryos subequal and nearly full sized but lying in reverse positions with their radicles directed toward micropyle and chalaza respectively).

### Euonymus macropterus Rupr.

*Dorsett & Morse 1336*, Odomari, Sakhalin (A): 10 seeds; 1 M; 9 P (six with 2, and three with 3 embryos).

### Euonymus oxyphyllus Miq.

*Wilson*, 1914, Hondo, Japan (A): 5 seeds, all from the same capsule; 2 M; 3 P (one with 2, one with 3, and one with 4 embryos).

### Euonymus vagans Wall. ex Roxb.

(*E. bockii* Loes.; *E. hupehensis* var. *brevipedunculatus* Loes.)

Seven seeds of two herbarium specimens were investigated.

*C. S. Fan & Y. Y. Li 673*, Hunan, China (A) [determined as *E. bockii*]: a single seed examined contained two subequal, full-sized and one minute embryo.

*Henry 9106B*, Yunnan, China (A) [determined as *E. hupehensis* var. *brevipedunculatus* Loes.]: 6 seeds; 2 M; 4 P (all 2-embryonate).

### Euonymus verrucosoides Loes.

Sixteen seeds of two herbarium specimens were examined.

*Wilson 3102*, Western Szechuan, China (A): 7 seeds; 1 M; 6 P (two with 2, three with 3, and one with 5 embryos; one 3- and the single 5-embryonate seed with only minute embryos).

*Rock 14978*, Southwestern Kansu, China (A) [determined as *E. verrucosoides* var. *viridiflorus* Loes. & Rehd.]: 9 seeds; 2 M; 7 P (one with 2, five with 3, and one with 4 embryos; one 3-embryonate seed with two equal, full-sized and one minute embryo).

## MONOEMBRYONATE SPECIES OF EUONYMUS

Since *Euonymus europaeus* has sometimes been mentioned as polyembryonate, the question of polyembryony in this species should be considered in some detail. Jäger (1814, p. 202) listed this species among a few plants in seeds of which two embryos occur. In order to verify Jäger's record Braun (1860, p. 156) examined seeds of *E. europaeus* and remarked, "Wenn hier nicht eine Verwechselung mit der folgenden Art [*E. latifolius*] im Spiel ist, so ist ein solches Vorkommen jedenfalls sehr selten, denn mir gelang es nicht bei dieser Art mehr als einen Keimling zu finden, wiewohl ich mehr als ein halbes Hundert Samen zergliederte."

In 1916, however, Bally reported the occurrence of polyembryony in *E. europaeus*. According to his observations, sometimes the embryo sacs in this species degenerate in an earlier or later stage of development. The space which was occupied by the embryo sac becomes surrounded by the nucellar tissue. The cell walls of these "tapetum-cells" dissolve themselves, and their naked contents wander into the cavity and soon fill in the latter with a homogeneous tissue as has been observed in the pollen sacs of certain monocotyledons. When the cavity is almost completely filled with nucellar tissue, the exterior layers of the latter in the micropylar region begin to execute divisions which lead to the development of one or more

embryos growing into the endosperm tissue. However, Andersson, on the basis of his own study of embryology in *E. europaeus*, criticized Bally's observations, saying (p. 30), "The nucellar cells can not be involved at all, because the nucellus disintegrates early and its small chalazal remainder is of no significance. . . . I believe that Bally's statement is to be attributed to defective staining" (translation supplied). Regarding Bally's explanatory account of the occurrence of adventitious nucellar embryony in *E. europaeus*, Andersson (p. 32) further remarks, "The formation of embryos in the micropylar region from the cells of the nucellus is impossible, since even this part of the nucellus disintegrates early. The origin [of embryos] from the cells of the inner integument would perhaps be possible [in this species], but I have never observed it. I also have not found polyembryony, and to my knowledge the latter has been observed [in this species] otherwise only once by Jäger (1814)."

The writer examined 30 seeds from each of two living cultivated specimens of *Euonymus europaeus* (Arnold Arboretum no. 18253, and Fairfield Garden Apts., Watertown, Mass., *Brizicky*, Oct. 1963) and found no evidence of polyembryony. Since Braun, Andersson, and the present writer have not found polyembryony in this species, one may assume either that Jäger's and Bally's records were based on misidentified material or that polyembryony in *E. europaeus* is extremely rare.

The following species investigated by the writer showed no polyembryony:

*Euonymus bungeanus* Maxim.: 30 seeds of a living specimen, Arnold Arboretum no. 2128-D (grown from seeds received from J. Hers, China, 1919).

*Euonymus maackii* Rupr.: 30 seeds of a living specimen, Arnold Arboretum no. 14563-1.

*Euonymus sachalinensis* (Schmidt) Maxim.: 15 seeds of a living specimen, Arnold Arboretum no. 13213-A.

*Euonymus semiexsertus* Koehne: 50 seeds of a living specimen, Arnold Arboretum no. 99-35-B.

*Euonymus yedoënsis* Koehne: 150 seeds of three living specimens, Arnold Arboretum no. 34340-A (cutting from Arnold Arboretum no. 14576-1-A), thirty seeds; Fairfield Garden Apts., Watertown, Mass., *Brizicky*, Oct. 1963, tree no. 1, ninety seeds, and tree no. 2, thirty seeds.

Although a few seeds, taken from random herbarium specimens of *E. atropurpureus* Jacq., *E. obovatus* Nutt., and *E. occidentalis* Nutt., were all monoembryonate, no conclusion can be made about the nature of these species until adequate material is investigated. Seeds of *E. fimbriatus* Wall. and *E. verrucosus* Scop. were found to be monoembryonate by Braun (1860).

Although the present investigations indicate that all the above-mentioned species may be monoembryonate, the monoembryony of at least some species, assumed on the basis of not very abundant material, should be reinvestigated. Furthermore, it seems to be of even greater importance to study the embryology of these species in order to determine the origin of the embryo, since even a single embryo within a seed could be apomictic.

## SUMMARY AND CONCLUSIONS

The occurrence of polyembryony in *Euonymus latifolius* and E. *americanus*, recorded in the nineteenth century, has recently been confirmed by Andersson (1931) for the former and by the writer for the latter species. On the contrary, polyembryony in *E. europaeus*, recorded by Jäger (1814) and Bally (1916) has not been substantiated (Braun, 1860; Andersson, 1931; the writer). If these records were not due to misidentification, polyembryony in *E. europaeus* may at least be extremely rare. I have found polyembryony to be of common occurrence in *E. alatus*, *E. dielsianus*, *E. macropterus*, *E. oxyphyllus*, *E. vagans*, and *E. verrucosoides*, all of eastern Asia. In *E. bungeanus*, *E. maackii*, *E. sachalinensis*, *E. semiexsertus*, and *E. yedoënsis* only monoembryonate seeds were observed. Although no polyembryonate seeds were found in *E. atropurpureus*, *E. obovatus*, and *E. occidentalis*, the material investigated was inadequate. Braun (1860) found *E. verrucosus* and *E. fimbriatus* also to be monoembryonate.

In the polyembryonate species the number of supernumerary embryos in a seed varies from one to nine. Only rarely are two or three embryos of a seed ± full sized and subequal; usually the supernumerary embryos are small to very minute. They are usually located with at least their radicles in the micropylar region and directed toward the micropyle (FIG. 1, a, f). In some cases, however (e.g., in *E. americanus*, *E. alatus*, *E. dielsianus*), one supernumerary embryo was lying in a reverse position with its radicle directed toward the chalaza (FIG. 1, b, c, g), and in a few cases one or more embryos were situated ± transversely (FIG. 1, d, e). In a few instances (e.g., in *E. verrucosoides*), a full-sized embryo was absent, but there were several minute ones in the micropylar region. The cotyledons of all the embryos of a seed usually lie in nearly the same longitudinal (vertical) plane, the position of which with regard to the raphe varies from one seed to another. Although sometimes parallel to the plane of the raphe, the plane of the cotyledons is more often at an angle to it.

Since Andersson showed that in *Euonymus europaeus* and *E. latifolius* the nucellar tissue disintegrates early and the adventitious embryos in the latter species arise from the inner integument of the ovule, one may assume that the early disintegration of the nucellus is a generic character and that in all polyembryonate species the adventive embryos originate from the inner integument. In fact, the integumental origin of the supernumerary embryos located in the micropylar region in seeds of the polyembryonate species of *Euonymus* can hardly be doubted. An identical origin of the embryos found in a reverse or ± transversal position is most probable, although the embryos at the chalazal end might also be of an antipodal origin (through apogamety). In one instance (*E. americanus*, *Wiegand & Manning 1908*), an endospermous origin of a reverse embryo is suspected.

Adventitious embryony from the inner integument seems to be relatively rare and has so far been recorded in only about ten species in nine

genera and eight families (Johansen, pp. 283, 284). In the family Celastraceae this kind of polyembryony is also known in *Celastrus scandens* L. It is notable that "for some reason, adventitious embryony seems to be relatively frequent in species native to warm temperate or tropical climates" (Stebbins, 1950, p. 384).

The question of whether a full-sized, normal embryo in polyembryonate seeds or a single embryo in monoembryonate seeds of *Euonymus* develops from a fertilized egg cell, or whether it is at least sometimes apomictic, can not be answered without detailed embryological study of the species involved. Andersson's statement (p. 34) regarding *E. latifolius* reads in translation, "I can ascertain that the fertilized egg cell dies in some cases. Whether it is always the case, I do not know. However, it is not to be denied that even in seeds with a single embryo this can be an adventitious one."

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# CONE MORPHOLOGY IN PINUS SABINIANA [1]

JAMES R. GRIFFIN

THE DIGGER PINE (*Pinus sabiniana* Dougl.) of California's foothill woodland, is unique in several ways. Few other pines can tolerate such sterile soils or xeric habitats, have such a diversity of irregularly shaped crowns, or show such impressive variation of cone forms within and between populations.

Cone morphology has been emphasized in all taxonomic accounts of *Pinus sabiniana*. After commenting on the branchy form of the crown, most authors mention the conspicuous "spurs" — as the combined umbo and apophysis of the basal cone scales will be termed here. A few authors have been impressed by extra long spurs in certain local populations. For example, Jepson (1909, p. 217) named one population on Mount Diablo having "strongly spur-hooked" scales and relatively long seed wings as variety *explicata*.

Early workers had insufficient material at their disposal to study geographical patterns in cone variation. Still, a few California botanists with wide field experience suggested some regional trends. Thus, Lemmon (1888) thought that the northern forms of the cone were less strongly spurred than the southern forms, adding that trees in the Tehachapi had large cones with strong hooks "closely approaching" *Pinus coulteri* D. Don.

The most detailed reference to cone variation in *Pinus sabiniana* was given by Stockwell (1939), who stated: ". . . the degree of variation in cone size and morphology exhibited by this pine is approached by few others." He also felt that this variation often fell into two patterns within the species as follows: "In central and northern California the cones of digger pine often resemble those of Coulter pine in size and general conformation. . . toward the southern end of its range, however, and near the coast, colonies of digger pine are known that produce an entirely different appearance. . . the general aspect of the cone is similar to that of Torrey pine. . ."

A broad study of this species was made and reported by the author in an unpublished doctoral dissertation (1962). As part of that study, cone samples from populations throughout the range of *Pinus sabiniana* were analyzed for many characters. Preliminary sampling had suggested that

[1] This paper is based on parts of a thesis submitted to the University of California in partial satisfaction of the requirements for the Ph. D. degree in botany. Portions of the study were supported by cooperative funds from the Pacific Southwest Forest and Range Experiment Station, Forest Service, U. S. Department of Agriculture, Berkeley, California.

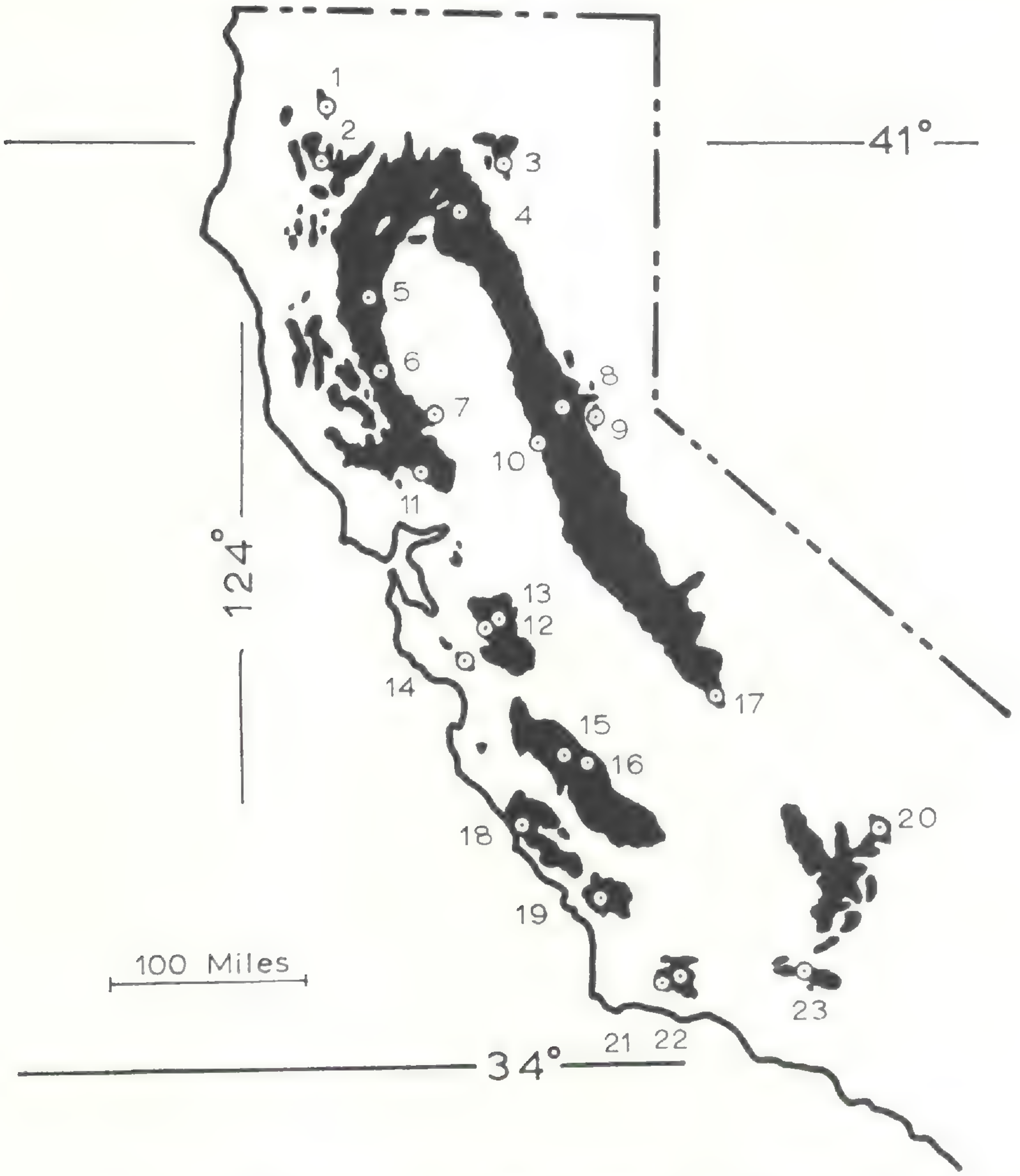


FIG. 1. Natural distribution of *Pinus sabiniana* in California. Circled dots indicate population sample locations; numbers offset from dots refer to sample descriptions in TABLE 1.

intra-tree variation in both size and form of cones was small in contrast to intra- or inter-population variation. To minimize the expected high variance within populations, trees of a "standard" size and age class were sampled. Resulting cone samples from the upper, lateral branches of standard trees were more comparable physiologically than samples from convenient ground reach would have been. Unfortunately, scarcity of standard trees in the field, as well as storage and handling problems in the laboratory, forced the major samples to be somewhat restricted — one cone from each of 20 different trees. In some localities only 10 cones were obtained. The natural distribution of the species and the relative location of samples appear in FIG. 1. In addition to population samples, the

complete cone crops on two trees in one population were collected for two consecutive years in order to estimate the nature and magnitude of intra-tree variation.[2]

## CONE SIZE

Stockwell (1939) suggested that a small-cone population existed on Figueroa Mountain in the southwestern corner of the range. "These examples," he emphasized, "are not of rare individual cones or of isolated trees, but of local races. . ." This note prompted Gaussen (1960) to describe forma *microcarpa*. Vague reports of other small cone populations in the Tehachapi Mountains in the southeastern corner of the range have circulated, although Lemmon alluded to large cones in the same region. Stockwell (1939) and Mason [3] had been impressed with large-cone populations in the northwestern portions of the range.

Preliminary sampling in this study suggested that a more detailed survey of cone size was desirable. Aside from the possibility of general cone size differences between populations, absolute cone size was investigated because of its influence on cone form, cone scale development, seed size, and other associated characters.

The spurs on many cones so complicated direct measurement of length or width on either open or closed cones that air-dried weight was selected as the size criterion. The results of the population survey appear in FIG. 2. No simple correlation of latitude, temperature, precipitation, or other habitat factor with cone size was apparent. The ranges of the largest and smallest samples just overlapped. Clearly, the larger and smaller samples are distinct from one another in a statistical sense, although many of the intermediate samples do not differ significantly from each other. The complete intra-tree analyses revealed that mean cone-weight per tree could vary at least 15 per cent in different years. The standard errors of the mean in FIG. 2 suggest the variable nature of many populations. Despite the high variances involved, the magnitude of difference between the more extreme samples suggests that some meaningful population differences exist.

The phenotypic differences expressed in FIG. 2 might be thought to reflect merely environmental differences — in part they must. But several factors suggest that genetic differences also are involved. One line of evidence supporting this view is found by comparing specific pairs of populations. For example, the Plummer Creek (#1) sample with the largest cones grew in a moderately unproductive "serpentine" habitat. The Applegate (#8) sample, with rather small cones, grew under a comparable precipitation regime, but on a more productive soil. General crown vigor in the two samples as measured by annual branch-length increments and

[2] Five cone subsamples from all collections are on deposit at the Institute of Forest Genetics, Placerville, California.

[3] H. L. Mason. Botany Department, University of California, Berkeley, California. Personal communication.

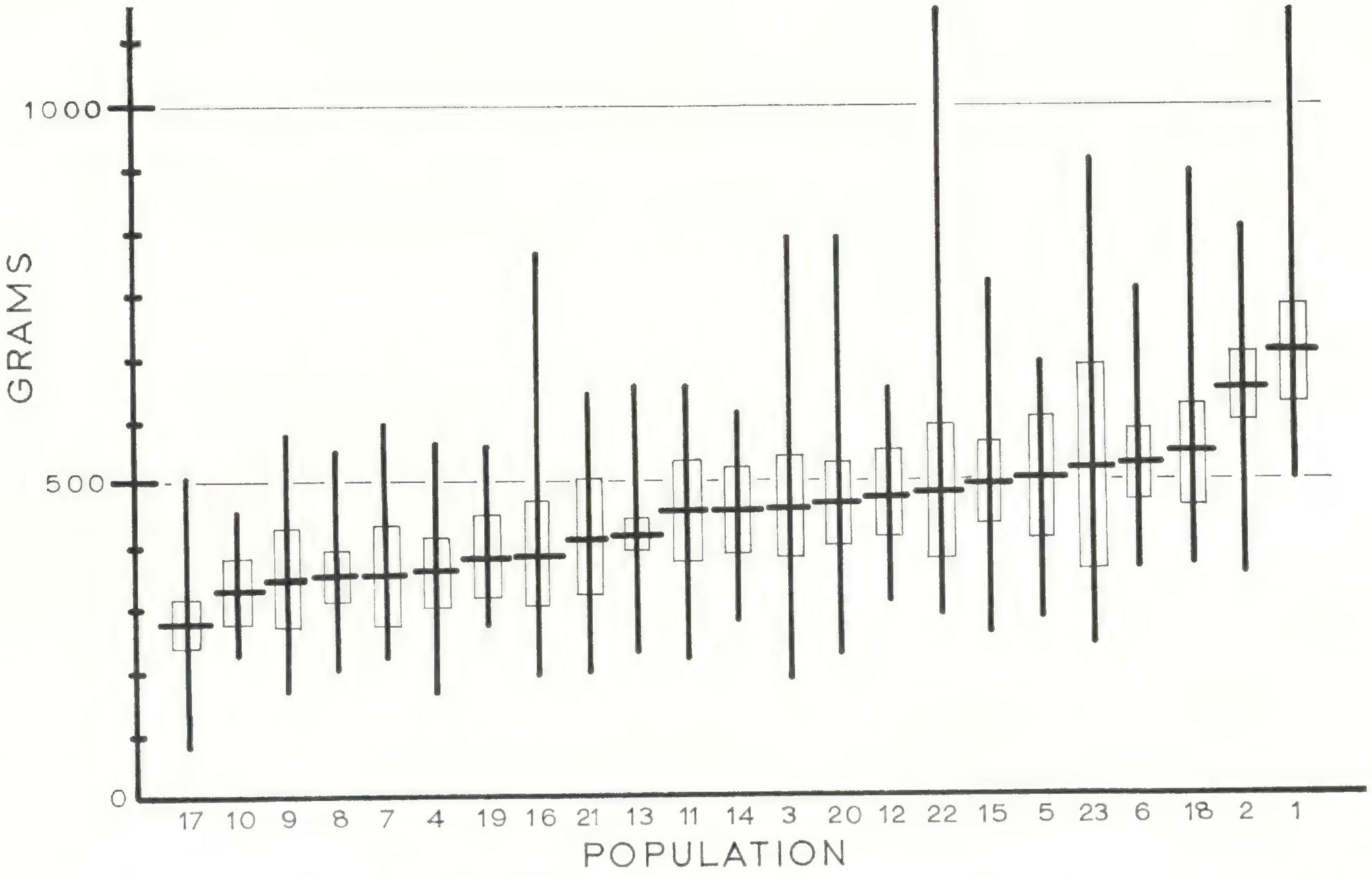


FIG. 2. Cone weight variation in *Pinus sabiniana*. Data are arranged in order of increasing mean weights. Horizontal cross-bars represent sample means, vertical bars represent sample ranges, and rectangular boxes indicate ± 2 standard error of the mean values. Population numbers refer to descriptions in TABLE 1.

TABLE 1. **Description of population sample localities**

| SAMPLE NUMBER | NO. CONES IN SAMPLE | LOCALITY | LATITUDE | LONGITUDE | ELEVATION | M.A.P.* |
|---|---|---|---|---|---|---|
| 1 | 20 | Plummer Creek | 41° 09′ | 123° 13′ | 2,400′ | 45″ |
| 2 | 20 | Big Bar | 40 45 | 123 13 | 1,300 | 47 |
| 3 | 20 | Murken Bench | 40 50 | 121 26 | 4,500 | 20 |
| 4 | 20 | Bear Creek | 40 31 | 122 04 | 1,200 | 35 |
| 5 | 10 | Bennett Creek | 39 49 | 122 39 | 2,000 | 25 |
| 6 | 20 | Summit Rock | 39 09 | 122 44 | 3,500 | 40 |
| 7 | 10 | Buckeye Creek | 38 55 | 122 01 | 200 | 17 |
| 8 | 20 | Applegate | 39 00 | 120 59 | 2,000 | 47 |
| 9 | 10 | Volcanville | 38 58 | 120 48 | 3,200 | 55 |
| 10 | 10 | Folsom Dam | 38 41 | 121 10 | 250 | 24 |
| 11 | 10 | Conn Dam | 38 26 | 122 20 | 300 | 30 |
| 12 | 10 | Mt. Hamilton-1 | 37 20 | 121 40 | 3,300 | 25 |
| 13 | 20 | Mt. Hamilton-2 | 37 21 | 121 37 | 3,900 | 30 |
| 14 | 10 | Uvas Creek | 37 06 | 121 45 | 800 | 25 |
| 15 | 20 | San Benito River | 36 23 | 120 57 | 1,800 | 15 |
| 16 | 20 | Clear Creek | 36 23 | 120 44 | 3,800 | 18 |
| 17 | 20 | Sycamore Creek | 36 53 | 119 15 | 1,800 | 23 |
| 18 | 20 | Redwood Gulch | 35 50 | 121 23 | 1,800 | 40 |
| 19 | 10 | Las Pilitas | 35 21 | 120 29 | 1,500 | 17 |
| 20 | 20 | Nine Mile Canyon | 35 52 | 118 00 | 6,500 | 10 |
| 21 | 10 | Figueroa Mt.-1 | 34 44 | 120 01 | 3,000 | 20 |
| 22 | 20 | Figueroa Mt.-2 | 34 44 | 119 49 | 3,700 | 23 |
| 23 | 10 | Cow Spring | 34 44 | 118 39 | 3,800 | 18 |

* Mean annual precipitation, estimated for most stations.

needle-lengths was similar. Tree height growth was superior in the Applegate stand. Small cones in this case seemed not to be a function of "poor" tree-growth, and conversely, large cones were not necessarily a function of "good" tree-growth.

No evidence of unusually small cones was found in the Figueroa Mountain region (see #21 and #22 in FIG. 2). Two samples were taken in the area — one (#21) located on the most sterile site available. The cones of sample #21 were smaller than the species mean; those of sample #22 were larger than the species mean. Ironically, the heaviest individual cone of any sample was found in the general "microcarpa" area in sample #22.

## CONE FORM

The shape of *Pinus sabiniana* cones varies widely, but population patterns were not clearly suggested in the samples. In large part the relationship of length to width depends upon absolute size. Many of the ovoid cones were larger than normal (FIG. 3). Although large cones have more massive individual scales, they also tend to have a greater number of scales per cone. The longer axis needed to accommodate the extra

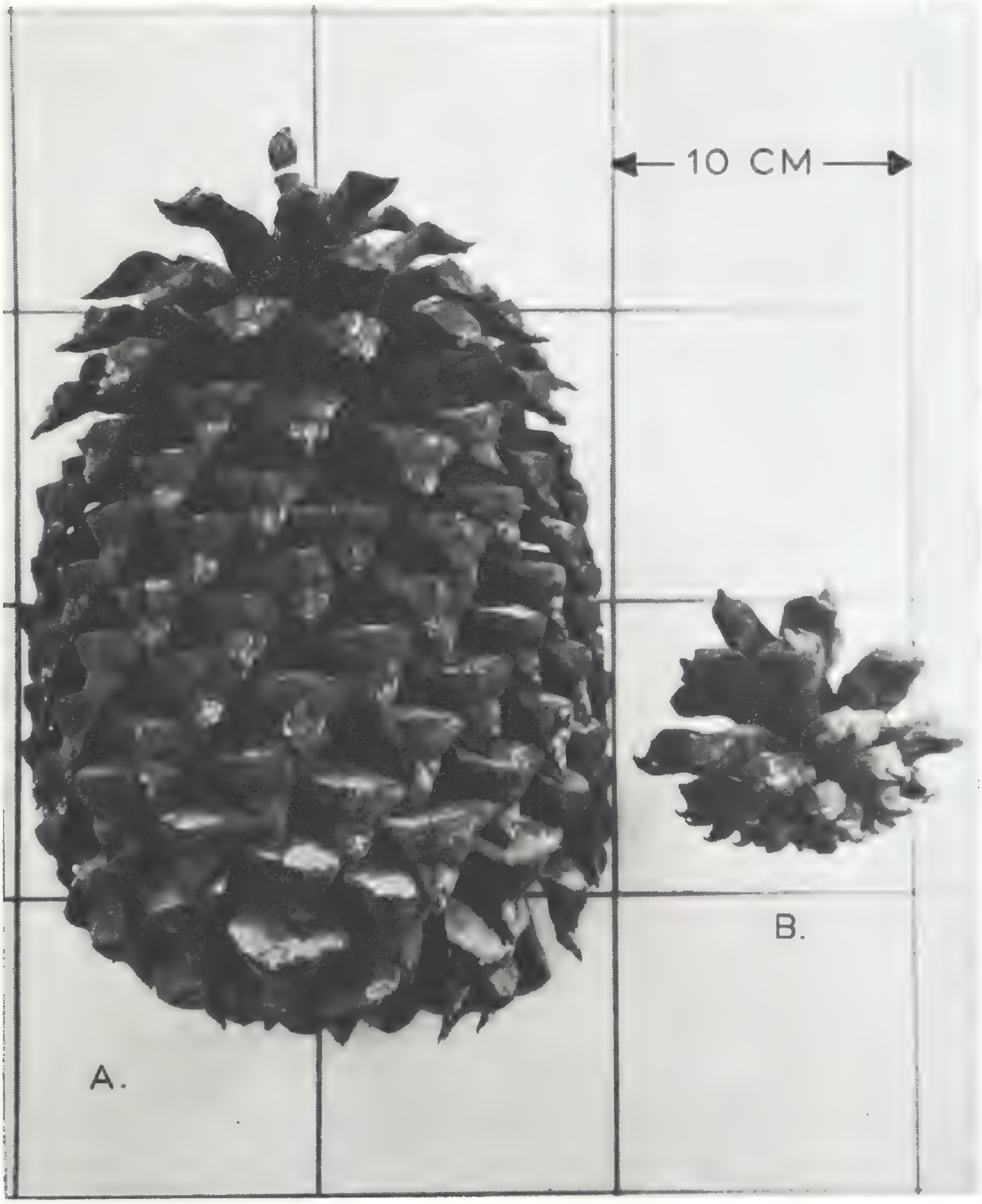


FIG. 3. Two cone form extremes in *Pinus sabiniana*. The elongated cone A has a greater number of scales than "normal," while the small spherical cone B has relatively few scales. The cones in FIG. 4 are of more usual shape.

scales of big cones makes the cones appear more cylindrical. On the trees that were intensively studied for two successive years, average cone weight decreased and average number of scales per cone decreased. The length-width ratios also shifted slightly with the decrease in cone size and scale number. In this case as cone size decreased, number of cones per tree increased.

No significant differences in phyllotaxis were noted in any of the hundreds of cones examined. The usual scale arrangement in the central portion of the cone consists of 8 obvious parastichies in one direction, and

FIG. 4. Two examples of spur variation within *Pinus sabiniana* populations. The pairs of cones came from comparable trees growing a few feet apart.

13 obvious parastichies in the other direction. This arrangement is essentially the 8/21 ratio in terms of classical phyllotaxy, and it is found in the cones of many other pines. There is a tendency for the "primary

spiral" to wind in one direction, but this sometimes varies between cones from the same branch.

## SPUR FORM

One of the most conspicuous features of cone variation in *Pinus sabiniana* is in relative spur length (Fig. 4). Although spur length is obvious on a given cone, the condition is rather difficult to quantify for a population. Absolute spur length is not a satisfactory measure, because it is affected by absolute cone size. In order to achieve a more independent criterion of spur development, a "spininess index" was assigned to each cone. This value was computed by measuring the length and width of one spur of constant relative position on the dorsal base of each cone. This length included both the umbo (the first year's external scale development) and the apophysis (the second year's extension growth of the cone scale). Spur length was divided into the width of the spur base. Spurs with values of 1.0 or greater were rather "blunt" (Fig. 3; Figs. 4B, 4D). Spurs with ratios of 0.5 or less were very "spiny" in aspect (Figs. 4A, 4C).

The differential scale-growth causing spiny cones is evident early in ontogeny. During the first season's growth of the cone, the spiny condition is obvious if it is to develop at all. The proportion of total number of scales that become spiny in a cone is variable. Occasionally all the scales are markedly affected (Fig. 5D), but more frequently only the more basal scales are affected (Figs. 5A, 5C). No practical way to describe the proportion of spiny scales in a cone was found. Spininess values refer only to the spininess at the basal portion of the cone. One feature of cone spininess, its stability within a given tree, is quite constant. If cones on a tree were spiny, every cone on the tree was spiny to the same degree year after year.

In addition to relative length, spurs vary greatly in degree of curvature. Some spurs are strongly recurved (Figs. 4A, 4C); others are straight except for the extreme tip of the umbo (Fig. 3A). Jepson (1910) long ago commented on such straight and recurved spur forms. Curvature seemed to be independent of spur length in many cases. In this survey each cone was assigned an arbitrary spur "curvature index." Only spurs of constant relative position on the dorsal base of the cone were used in assigning curvature values. Cones with the straightest spurs were classed "1"; cones with the most recurved spurs as "5." Intermediate values were assigned, with some difficulty, to intermediate conditions. As with spur length the degree of curvature was rather constant within all cones of a tree year after year.

The results of the spur survey are difficult to interpret. Geographic patterns in spininess or curvature are obscured by variation within a population. Very spiny cones were found infrequently in most of the populations sampled. In the area on Mount Diablo of Jepson's var. *explicata*, for example, several trees with very spiny cones were observed. Small samples in the vicinity suggested that no spiny "population" was involved.

TABLE 2. **Spininess variation of several cone samples, by populations**

| POPULATION | FREQUENCY DISTRIBUTION WITHIN SPININESS INDEX CLASSES | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 0.3 | 0.4 | 0.5 | 0.6 | 0.7 | 0.8 | 0.9 | 1.0 | 1.1 | 1.2 |
| PLUMMER CREEK (#1) | | | | 1 | 2 | 3 | 5 | 7 | 1 | 1 |
| FIGUEROA MT. (#22) | | | 2 | 4 | 6 | 3 | 2 | 2 | 1 | |
| BIG BAR (#2) | 1 | 2 | 11 | 5 | 1 | | | | | |
| APPLEGATE (#8) | | 9 | 5 | 3 | | 2 | | | | |

TABLE 3. **Curvature variation of several cone samples**

| POPULATION | FREQUENCY DISTRIBUTION WITHIN CURVATURE INDEX CLASSES | | | | |
|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 |
| PLUMMER CREEK (#1) | 12 | 6 | 2 | | |
| FIGUEROA MT. (#22) | 2 | 4 | 11 | 2 | 1 |
| BIG BAR (#2) | | 4 | 9 | 2 | 5 |
| APPLEGATE (#8) | | | | | |

The sampling intensity was not great enough for strong quantitative conclusions, but the frequency of some combinations of spur characters does suggest population differences (TABLES 2, 3). Two of the more extreme patterns in cone morphology are compared in FIG. 6 in which weight, spininess, and curvature of all cones in two samples are plotted. A common spur situation in the species seems to be wide variation around intermediate spininess and curvature values. In FIG. 6 the Plummer Creek cones represent a skew toward straight, blunt spurs, while the Applegate data is skewed somewhat in the direction of curved, attenuated spurs. Of all the populations sampled, Plummer Creek had the most distinctive spur pattern. This population is also one of the most effectively isolated stands in the scattered Klamath Mountain populations. The blunt spurs of the Plummer Creek cones contrasted sharply with the spiny cones of the Big Bar (#2) sample 35 miles away on the other side of the Trinity Alps (see modal spininess values in TABLE 2).

One population which had an unusual display of cone size, form, and spur variation was Clear Creek (#16). Three facts about this region should be mentioned. First, the edaphic situation is extreme with an extensive area of highly serpentinized parent material occurring under a relatively low rainfall. Secondly, the mixture of pine species (*Pinus sabiniana*, *P. coulteri*, and *P. jeffreyi*) occurs nowhere else. *Pinus sabiniana* grows with *P. coulteri* in many other areas in the south and with *P. jeffreyi* in the north, but all three grow together only near Clear Creek. Thirdly, the morphological variation in these three species is quite high here.

When Zobel (1951) studied introgression between *Pinus coulteri* and *P. jeffreyi*, he found the greatest array of cone variation in his "pure"

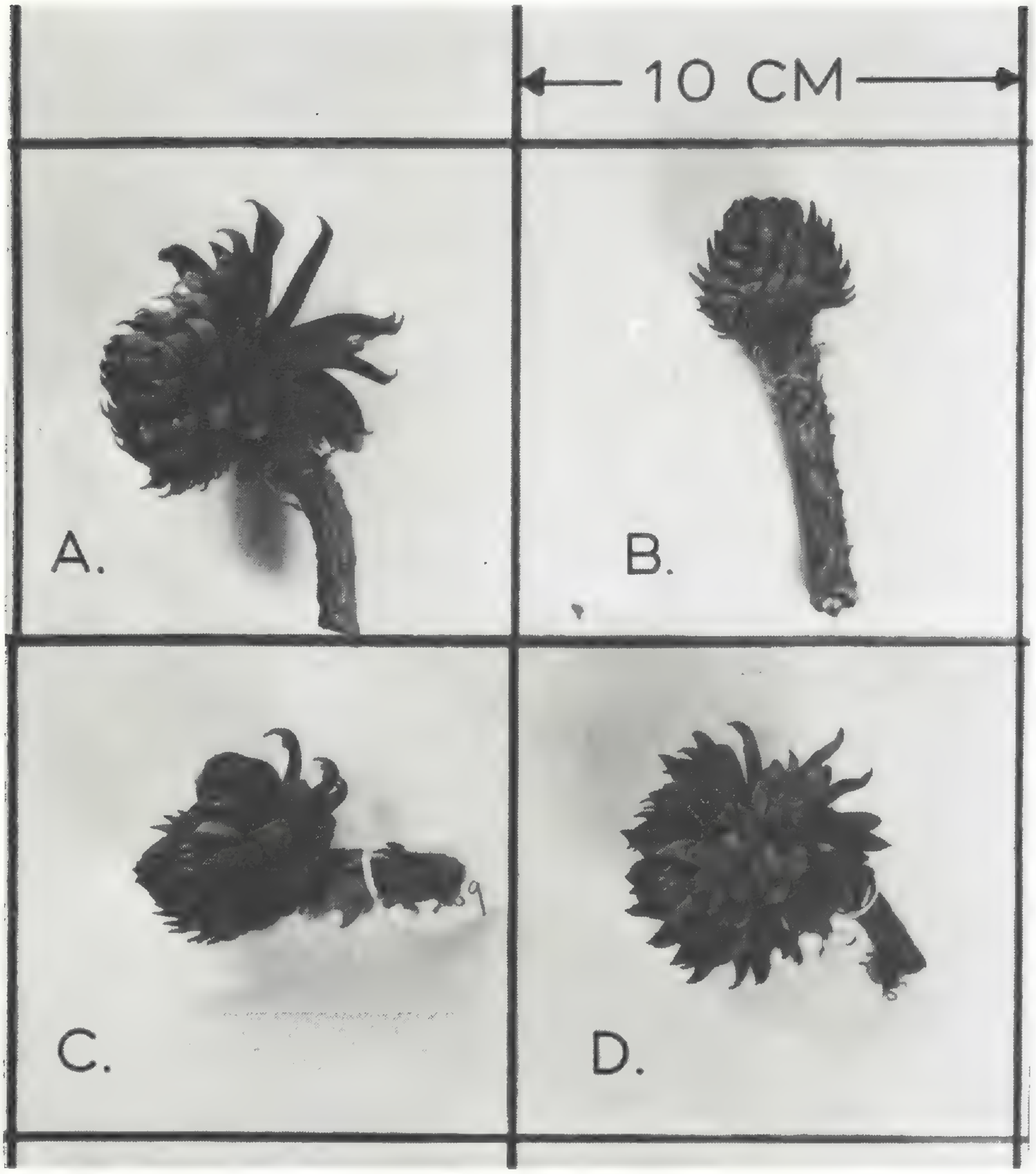


FIG. 5. Umbo variation in four normal, healthy *Pinus sabiniana* cones at end of first season's growth. Cones A and B came from trees growing a few feet apart.

Coulter and Jeffrey samples in this area. This study also showed very large morphological diversity in *Pinus sabiniana*. Zobel speculated that *Pinus sabiniana* in some way may have been involved in the great Jeffrey-Coulter variation at Clear Creek. This possibility must be seriously considered. However, the extreme nature of the habitat also may have contributed to the variation in cone form in all three species. The relative influence of the associated pines and the unique habitat on *Pinus sabiniana* variation must remain speculative.

Many authors have remarked that *Pinus sabiniana* cones occasionally resemble *P. coulteri* cones. The attenuation and curvature of the basal spurs on cones of the two species are often identical. The basic difference is that obvious spur development in *Pinus sabiniana* is often restricted to

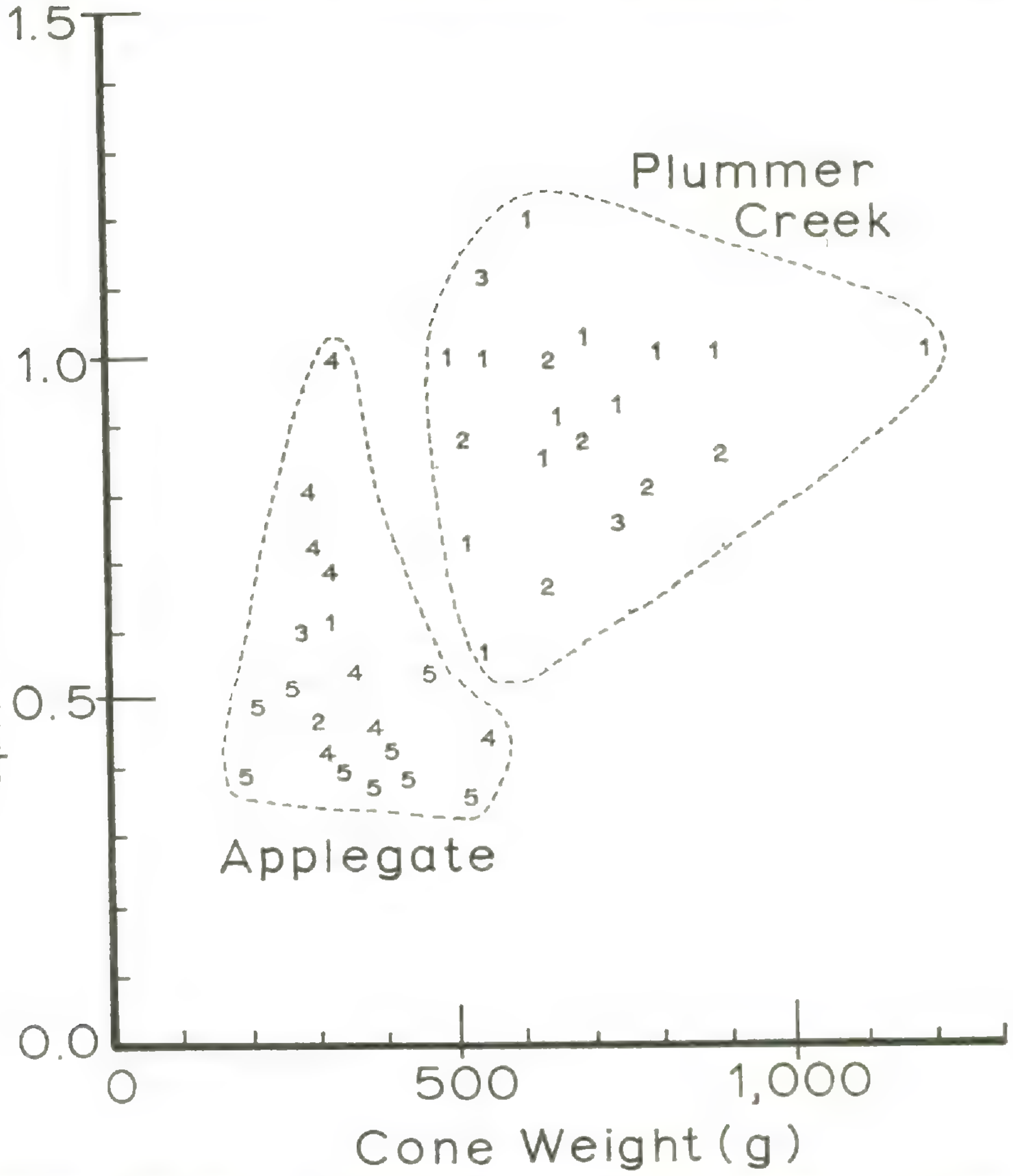


FIG. 6. Relationship of Plummer Creek (#1) and Applegate (#8) cone samples. Each plotted figure represents the curvature value for one cone of given spininess and weight.

the basal portion of the cone, while in *P. coulteri* hooked spurs commonly extend to the cone apex. No clear geographical pattern to Coulter-like cones was suggested by the limited sampling here.

A less well known aspect of *Pinus sabiniana* morphology is the occasional resemblance of cones to those of *Pinus torreyana* Parry. Stockwell's observations of Torrey-like cones were confirmed in several southern California localities. On one tree, cones with weakly developed spurs over the whole surface were essentially indistinguishable from cones of *Pinus torreyana*. *Pinus torreyana* has long been isolated from *P. sabiniana*, being restricted to local coastal situations in southern California. Interestingly, the particular Torrey-like cones mentioned above were from the only coastal population of *Pinus sabiniana* (Redwood Gulch, #18). One near-

definitive character that separates *Pinus sabiniana* and *P. coulteri* cones — the relative length of seed and seedwings — is not helpful in separating cones of *Pinus sabiniana* and *P. torreyana*, because the characters of seed and wing in these species overlap.

## SPECIFIC GRAVITY

Since four of the samples were from stands where *Pinus sabiniana* grew with *P. coulteri*, cone specific gravities were taken to compare with the values Zobel (1951) reported for *P. coulteri*. He had found specific gravity helpful in characterizing cones of *Pinus coulteri*, and its hybrids with *P. jeffreyi*. All the *Pinus sabiniana* sample means were significantly different from Zobel's *P. coulteri* means. But the *Pinus sabiniana* values did overlap into the *P. coulteri* range. Specific gravity might be helpful in separating *Pinus sabiniana* and *P. coulteri* cones, but large samples and careful analyses would be required.

The specific gravity survey was later expanded to include all cones collected, and it was found that this physical character of the cones was loosely associated with latitude. Northern samples had lower specific gravities than southern samples (TABLE 4). With only minor deviations the intervening populations had intermediate values.

Although the experimental methods (by water displacement) were crude, they were reproducible. Successive annual sampling in the Applegate trees gave similar results despite changes in cone size. The two Figueroa Mountain samples had virtually identical specific gravity distributions as did the two independent samples at Mount Hamilton. Why the latitudinal trend in values was found or even why different samples from the same local area were so similar is not clear. Critchfield (1957) found specific gravity helpful in characterizing regional cone variation within *Pinus contorta*. But his specific gravity data were related to such morphological features as serotinous habit. Here, no relation to obvious morphological characters or habitat was apparent.

TABLE 4. **Specific gravity of cones from several samples**

NORTHERN SAMPLES

| POPULATION | MEAN SPECIFIC GRAVITY | RANGES OF SPECIFIC GRAVITY |
|---|---|---|
| MURKEN BENCH (#3) | 0.70 | 0.59–0.79 |
| BIG BAR (#2) | 0.71 | 0.65–0.81 |
| PLUMMER CREEK (#1) | 0.73 | 0.68–0.79 |

SOUTHERN SAMPLES

| | | |
|---|---|---|
| FIGUEROA MT. (#22) | 0.82 | 0.71–0.88 |
| CLEAR CREEK (#16) | 0.84 | 0.76–0.88 |
| REDWOOD GULCH (#18) | 0.85 | 0.77–0.96 |

## CONE COLOR

The magnitude of cone color variation in this species has never been described adequately. Color extremes were quantified by using Munsell soil color notations (Soil Survey Staff, 1951). These standardized soil colors conveniently covered the whole range of colors encountered in mature, unweathered cones.

Modal cone color varied from reddish brown (5 YR 4/4) to dark reddish brown (5 YR 3/3). Lightest extremes were: yellow (2.5 Y 7/6) and yellowish brown (10 YR 5/4). Darkest extremes were brown (7.5 YR 5/8), and dark red (2.5 YR 3/6). Cone color within a tree was relatively constant, and color appeared to be stable on a given tree year after year. The common color is clearly a reddish brown. Color variations are stressed because of the tendency one might have to attribute occasional yellowish *Pinus sabiniana* cones to introgression from the yellow coned *Pinus coulteri*. From the limited sampling here, the striking color deviations suggested no geographic pattern. Yellowish or reddish cones appeared in low frequency in all parts of the range. Some yellowish *Pinus sabiniana* cones appeared in mixed forests containing *P. coulteri*; others appeared far removed from *P. coulteri*.

## CONCLUSIONS

As a species, *Pinus sabiniana* seemed quite distinct from other "related" California pines with which it grows. No clear suggestion of introgression between this species and *Pinus coulteri* or *P. jeffreyi* was encountered in the field. Despite the wide range of habitat conditions in which the species grows, there was a general impression of uniformity in the appearance of the tree. In this context of tree similarity, the variation in cone features was impressive. The irregular pattern of this variation made it difficult to characterize the cones of local populations or to detect geographic trends within the species. A few small samples could lead to very erroneous generalities about *Pinus sabiniana* cones. With this in mind the following generalities are cautiously given:

(1) Large cones were frequently found in the North Coast-Klamath ranges; they may be elongated in form.

(2) Small cones were frequently found in the Sierra Nevada; they may be more ovoid in form.

(3) Cones with low specific gravity were frequent in the north; low specific gravity was not closely related to the larger size of northern cones.

(4) Cones with high specific gravity (overlapping into the range of *P. coulteri*) were found in the south.

(5) Spur form was quite constant within a tree but quite variable within and between population samples.

(6) Plummer Creek, a small isolated Klamath Mountain population, had a high frequency of blunt, straight spurs.

(7) Cones were occasionally quite similar in size, color, and spur form to those of either *Pinus coulteri* or *P. torreyana*.

This study of cone morphology when combined with other investigated features suggested that Jepson's variety *explicata* and Gaussen's forma *microcarpa* were based on characters derived from inadequate sampling and are not useful. Distinguishable geographic groupings of populations were not obvious within the variable species.

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PACIFIC SOUTHWEST FOREST AND RANGE EXPT. STA.,
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# THE ELAEAGNACEAE IN THE SOUTHEASTERN UNITED STATES [1]

SHIRLEY A. GRAHAM

ELAEAGNACEAE A. L. de Jussieu, Gen. Pl. 74. 1789, "Elaeagni," nom. cons.

(OLEASTER FAMILY)

The family is easily recognized and homogeneous, consisting of three genera, *Hippophaë* L., *Shepherdia* Nutt., and *Elaeagnus* L., all characterized by a dense covering of silvery or rusty, peltate or stellate hairs on the flowers, twigs, and leaves; 2–4-merous flowers lacking petals; and a fleshy or mealy berry- or drupelike accessory fruit derived from the accrescent floral tube. Only *Elaeagnus* is represented in our area. Nelson and Fosberg considered the family to be unigeneric, recognizing only *Elaeagnus*.

The genus *Hippophaë*, sea-buckthorn, of Europe and Asia, is distinguished by alternate leaves, unisexual flowers with a two-lobed floral tube, four stamens, poorly developed nectaries, and a long stigma. Generally, only *H. rhamnoides* L., composed of three subspecies, is recognized. In subsp. *rhamnoides* two races have been described, the one diploid ($2n = 12$), the other tetraploid ($2n = 24$). A count of $2n = 20$ has also been reported for the species. The orange flesh of the "fruit" is reported rich in vitamin C. Vegetative multiplication is common by means of underground stems.

The buffalo-berries, *Shepherdia*, comprising three North American species, have opposite leaves, unisexual flowers, a four-lobed floral tube, eight stamens, a ring of eight nectariferous glands in the floral tube at the base of the calyx lobes, and a short stigma. Chromosome numbers are known for *S. canadensis* Nutt., $2n = 22$, and for *S. argentea* Nutt., $2n = 26$.

On the basis of anatomy, *Hippophaë* and *Shepherdia* are considered by Servettaz to be more closely related to each other than to *Elaeagnus*. The family is most commonly placed in the Myrtales next to the Thymelaeaceae. It also shares several characters with the Proteaceae and Penaeaceae. Hutchinson alone closely relates the Elaeagnaceae to the Rhamnaceae.

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and Gray Herbarium made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. The scheme follows that outlined at the beginning of the series (Jour. Arnold Arb. **39**: 296–346. 1958). The area covered in this, as in former treatments, is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. Material included in the descriptions in brackets applies to species outside this area, and references marked by an asterisk have not been verified by the author.

Clusters of root nodules are commonly formed in all three genera through infection of developing lateral roots by an unidentified endophyte. The causal organisms have been variously interpreted as filamentous fungi, nitrogen-fixing bacteria, actinomycetes, and myxomycetes, but their identity is still unknown due to difficulties in isolating and culturing them. The endophyte is soil borne and must be reintroduced into the plants of each new generation. It is apparently capable of fixing nitrogen and in this way maintains a symbiotic relationship with its host, much as do bacteria associated with legumes. The only other nonleguminous angiosperm genera known to bear root nodules are *Coriaria*, *Myrica*, *Alnus*, *Casuarina*, *Ceanothus*, and *Discaria*; in none of these has the endophyte been positively identified.

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1. **Elaeagnus** Linnaeus, Sp. Pl. 1: 121. 1753; Gen. Pl. ed. 5. 57. 1754.

Shrubs or rarely trees, with alternate, unarmed or spiny branches, densely covered with silvery or brownish stellate or peltate hairs (scales). Leaves alternate, deciduous or persistent, petiolate, lanceolate to oblong or ovate, simple, entire, exstipulate, both sides or only the lower (abaxial) side covered with peltate hairs. Flowers regular, bisexual or unisexual (the plants then polygamo-dioecious), pedicellate, solitary or clustered in the axils of leaves or deciduous bracts, 4-merous. Floral tube cylindrical to globose at base, slightly contracted at apex of the ovary, then flaring and cylindric to campanulate above, the portion surrounding the ovary persistent, accrescent, the portion above deciduous in fruit; calyx lobes 4, silvery or rusty on the outer surface, yellow within; nectariferous disc cone- or cup-shaped, surrounding the base or diffuse at the base of the style. Petals none. Stamens 4, at the base of and alternating with the calyx lobes; filaments very short; anthers versatile, introrse, 2-locular, dehiscing longitudinally. Gynoecium 1-carpellate, superior, but often appearing inferior by contraction of the floral tube at the base of the style, free in the tube; stigma unilateral; style linear, canaliculate; ovary 1-locular, 1-ovulate, with basal placentation; ovule anatropous, 2-integumented. Fruit berry- or drupelike, the outer layers of the persistent floral tube fleshy or mealy, the inner layer hard and strongly 8-striate or leathery to membranaceous with very weak striations, ellipsoid, with or without hairs on the inner surface, surrounding a membranaceous achene. Seed 1, with little or no endosperm; embryo large, straight, the cotyledons fleshy. Embryo sac development of the normal (Polygonum) type. LECTOTYPE SPECIES: *E. angustifolius* L.; see Britton & Brown, Illus. Fl. No. U.S. ed. 2. 2: 575. 1913. (Name from Greek, *elaia*, olive, and *agnos*, the classical name for the chaste-tree, *Vitex agnus-castus*.[2]) — OLEASTER, RUSSIAN OLIVE, SILVERBERRY.

[2] The Greek feminine word *agnos* was adopted by Linnaeus and the ending altered to the Latin masculine *-us*. The gender of *Elaeagnus* is, therefore, masculine and not feminine as regarded in most taxonomic literature. (See Art. 73, sect. 2(2), Int. Code Bot. Nomencl. 1961.) The Latin word *agnus*, lamb, should not be confused with the altered Greek word. According to Linnaeus (Critica Botanica, pp. 127, 128. 1737; transl. by A. Hort, 1938, pp. 100, 101), "He [Gaza] translated Greek names into Latin according to the meaning. For example, *Vitex* was called in Greek *Agnos*,

A taxonomically difficult genus of about 40 species, including many subspecies and varieties, placed by Servettaz in sect. ELAEAGNUS (§ *Deciduae* Serv.), defined as spring-flowering with deciduous leaves, and sect. SEMPERVIRENTES Serv., comprising fall-flowering species having evergreen leaves. The genus is best represented in the steppe regions of Asia and in southern Europe; *E. commutatus* Bernh. (*E. argenteus* Pursh, not Moench), $2n = 28$, is native to Canada and the northern United States. Three Asiatic species cultivated in the southeastern United States have become naturalized to varying degrees in scattered localities. *Elaeagnus pungens* Thunb. (sect. SEMPERVIRENTES), $2n = 28$, is established in North and South Carolina and Tennessee. *Elaeagnus umbellatus* Thunb., $2n = 28$, (flowers in axillary umbel-like clusters) and *E. multiflorus* Thunb. (flowers solitary or paired in the axils), both of sect. ELAEAGNUS, occur in isolated populations as escapes.

Definition is difficult in many of the European and Asiatic species because of the morphological variability displayed over the extensive and ecologically diverse parts of their ranges. The presence of juvenile and adult leaves and the change in form of the fruit with maturation add to the difficulty. Development of spiny branches is most pronounced under dry, poor soil conditions and in young plants.

Several species are cultivated for their handsome silvery foliage and decorative red or silvery fruits; the Russian olive, *Elaeagnus angustifolius*, $2n = 12, 28$, is one of the most widely planted. Forms with variegated leaves are available in a few cultivated species.

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that word in Greek signifying *castus*; hence Gaza called *Vitex 'Castus'* instead of *'Agnus.'*

"The barbarians who followed him supposed *agnus* to be actually a Latin word, a synonym for 'sheep': hence they took *agnus* as a substantive and *castus* as an adjective, as *ovis casta* or *agnus castus*; and this nomenclature specially pleased the Pharmacists, though none more barbarous could have been found. From *Agnus* also is formed *Elaeagnus*, as it were *Olea-Vitex*: hence the right spelling is *Elaeagnus*, not *Elaeachnus*."

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# NOTES ON ROSACEAE IN THE LESSER ANTILLES

Richard A. Howard

The notes which follow illustrate some of the problems encountered in the slow task of preparing a flora for the islands of the Lesser Antilles. Much of the field work on which the discussion below is based was supported by grants from the National Science Foundation. I am grateful, as well, to the director and staff of the Muséum National d'Histoire Naturelle, Paris, for the opportunity of studying several historical collections which have long been unidentified.

**Chrysobalanus cuspidatus** Griseb. ex Duss, Fl. Phan. Antill. Fr. 258. 1897; Griseb., Fl. Brit. West Indies 711. 1864 (*nomen*); Urban, Symb. Antill. **5**: 351. 1907.

*Licania oligantha* A. C. Smith, Jour. Arnold Arb. **28**: 333. 1947, *syn. nov.*

In a small section of his Flora of the British West Indies, following the list of corrections and preceding the Index, Grisebach published a "List of species received since the impression of the first volume." Included among these names are a dozen epithets, each followed by: "Gr. (n. sp.)," the country of origin, and the collector. Not one of these names is accompanied by descriptive data and none can be considered validly published. All of them, however, have been cited in subsequent publications dealing with the West Indies or have been indexed in various works and attributed to Grisebach. Each offers difficult problems of citation and typification; *Chrysobalanus cuspidatus* will serve as an example.

This name was published by Grisebach who indicated (by an exclamation mark) that it represented a new species he had seen collected by Imray in Dominica. In the January 27, 1897, issue of Botanisches Centralblatt, E. Küster published an article on the anatomical characters of the Chrysobalaneae in which he referred to "Chr. cuspidatus Griseb." He cited an Eggers collection (edit. *Toepffer 618*) and a description of the upper epidermis and of the hairs (p. 137), although earlier in the text he had considered additional anatomical details. Although a protologue in all senses, this is regarded as an inadequate description of the species.

Also in 1897, and presumably later in the year, Duss published a treatment of the plants of Guadeloupe and Martinique and supplied a more usual description of *Chrysobalanus cuspidatus* which he attributed to Grisebach. Duss cited two of his own collections from Guadeloupe, *3476* and *3633*, and one from Martinique, *154*. The identification of much material Duss collected and cited was made or verified by Urban, and the original collections were deposited in Berlin. In 1907 Urban included

*Chrysobalanus cuspidatus* in a list of new genera and species, attributing the name to Grisebach and supplying a Latin description. He cited only two of the three specimens Duss had listed and the Eggers collection Küster had cited. There are, therefore, four possible authors but the correct citation of the name should give credit to Duss for the first published description of taxonomic value and should be — *Chrysobalanus cuspidatus* Griseb. ex Duss.

The identification of a holotype or the selection of a lectotype of *Chrysobalanus cuspidatus* is more difficult. The Imray specimen from Dominica, cited by Grisebach, is in the herbarium at the Royal Botanic Gardens, Kew, but this collection was not cited by any of the three men who published a description of the species. Duss did not select a holotype from the three collections he cited, nor did Urban from among the collections he mentioned. Regrettably no material studied by Duss or Urban could be located at the herbarium in Berlin, so the eventual selection of a lectotype is left to a future worker who, having material on loan from various institutions, can select the collection and the most complete specimen to represent the species.

In addition to its previously reported distribution from Guadeloupe, Dominica, and Martinique the range of this species can be extended to St. Lucia on the basis of collections of three individuals. Material collected by John Beard in St. Lucia during the years of the second world war was identified by A. C. Smith. Two of Beard's collections, *488* and *492*, were identified as a new species, *Licania oligantha*. A study of the cited material indicates an older description has been overlooked and *Licania oligantha* may be considered a synonym of *Chrysobalanus cuspidatus*. Subsequent to Beard's work additional material was collected in St. Lucia by R. A. Howard (*11638*) in 1950 and G. R. Proctor (*21621*) in 1959. This species, however, is still not represented by fruiting specimens and until that time its correct generic assignment is questionable. The field notes supplied by Beard from his collection *492*, the type of *Licania oligantha*, describe the fruit as blue and attractive to birds. An annotation on the type sheet, however, indicated the fruit was not received with the collection and was lacking for the description published by Smith.

A comprehensive study of the genera *Chrysobalanus*, *Licania* and *Moquilea*, at least as they occur in the western hemisphere, is needed. The majority of recent floras have considered *Moquilea* synonymous with *Licania* and have recognized *Chrysobalanus* as a distinct genus. Distinctions between these two genera are suggested to be in the length of the inflorescence, or the number of flowers, or in the habit of the plant. *Chrysobalanus* is considered by some to be monotypic; other authors suggest three to seven species may comprise the genus. *Chrysobalanus icaco*, the type species, is admittedly polymorphic and of wide distribution. The fleshy blue colored fruit of typical *C. icaco* is different from the fruit of species of *Licania*. Beard's description suggests a typical *Chrysobalanus* fruit for *Licania oligantha*. Smith did not consider *Chrysobalanus* in his discussion of the relationships of *Licania oligantha*. This species with the

missing fruit may prove to be intermediate between typical *Chrysobalanus* and typical *Licania*. Once again, more material is needed and a detailed study not only of the variation of *Chrysobalanus icaco* wherever it occurs, but of the relations of the three genera *Chrysobalanus*, *Licania* and *Moquilea*.

**Potentilla anglica** Laicharding, Veg. Eur. 1: 475. 1790.

*Potentilla procumbens* Sibth., Fl. Oxon. 162. 1794.

I can find no modern published record of the genus *Potentilla* in the Lesser Antilles. *Potentilla argentea* was listed as a cultivated plant in the Botanic Garden of St. Pierre, Martinique, in 1829 (De l'Horme, Ann. Marit. Col. 1: 142. 1830), but apparently has not survived in cultivation anywhere in the area. In an old collection sent to me for determination is a specimen collected by Belanger in 1857. Although no specific locality is given, Belanger was director of the St. Pierre Botanical Garden between 1853 and 1881, and the specimen which is *Potentilla anglica* was presumably a weed in the garden. Subsequent collectors have not recorded this species from the French islands but another unidentified collection, *W. H. & Barbara T. Hodge 2157*, made on Dominica, is the same species. The Hodges record their collection as "a weed in moss in which roses sent from England were packed; only a few plants seen in a rose bed at Fern Villa, Ridgefield Estate." Recent visitors have checked this location and failed to find the species established as a weed.

Elsewhere in the West Indies *Potentilla reptans* L. was collected by Brown and Britton in Bermuda, in 1905, and has not been recollected. *Potentilla anglica* (as *P. procumbens*) was also collected by Harris above New Castle in Jamaica, in 1915, but has not appeared in recent collections from that island. With such scattered records, one questions the necessity for considering species of *Potentilla* in a floristic treatment of the Antilles.

**Rubus ferrugineus** Wikström, Sv. Vet.-Akad. Handl. 1827: 68. 1828.

Two recent collections from the island of St. Kitts appear to be best referred to this poorly represented species. Wikström described *Rubus ferrugineus* basing it on a Forsström collection from Guadeloupe. All subsequent authors have failed to consider the species with the single exception of Rydberg who included *Rubus ferrugineus* as a species endemic to Guadeloupe in his treatment of the genus in the *North American Flora* (22: 449. 1913). Unfortunately the description given by Rydberg is puzzling for he cited no specimens, and yet included details not given in Wikström's original diagnosis. Two years later Rydberg (Bull. Torrey Club 42: 136. 1915) assigned to this species a collection, *Duss 2215*, from Guadeloupe and a collection, *Nelson 3305*, from Mexico. The Duss collection was originally identified as *Rubus jamaicensis* Sw. and so cited by Duss (Fl. Phan. Fr. Ant. 260. 1897), who indicated the plant was rare, being known from but one location on Guadeloupe and not reported

from Martinique. Dr. and Mrs. Henri Stehlé, residents of Guadeloupe, who have collected extensively in the French West Indies, have been unable to relocate the species and, in a most recent reference to the Rosaceae, list only the original Duss collection under the same specific determination given by Duss. (H. & M. Stehlé and Quentin, Fl. Guad. Depend. et Mart. 2: 53. 1949). Neither Urban in his *Symbolae Antillanae* nor L. H. Bailey in his series of papers on *Rubus* refer to the Wikström species or the type collection by Forsström.

In 1950 I visited St. Kitts and had the pleasure of going into the montane forests of that island with the late Malcolm Smith. Instead of taking the routine trail up Mt. Misery, that excellent naturalist suggested a new route previously unbotanized which led through a palm break across a knife-like ridge into a mossy forest and finally, by a short descent, to a small crater lake called Dodan's Pond at 2750 feet on Verchild's Mountain. Mr. Smith explained there was a conflict regarding the existence of that pond which is reflected even in its name. Either the pond had been difficult to locate in former years and its existence was doubted, or the pond was evanescent, perhaps appearing in alternate years, for an optional spelling of the location he suggested was Dos d'Ans. At the edge of the pond and in a thicket of vegetation was a colony of blackberry plants. These had long weak trailing sterile stems and arching fertile ones capped with panicles of many flowers and excellent flavored small fruits. The specimens collected (*Howard 11962*) could not be associated with any known species from the Antilles, native or introduced, and additional material was needed. In 1959 Mr. Smith and George Proctor again visited Dodan's Pond and recollected the *Rubus*. At first it seemed the material represented a new species. It was similar to *Rubus florifolius* Bailey of Hispaniola but had a single terminal panicle, smaller prickles, and longer sepals. It lacked the coriaceous leaves and glabrous pistils of *Rubus florulentus* Focke of Puerto Rico. Rydberg's modern description of *Rubus ferrugineus* was then checked against the more general original description published by Wikström. Although a Forsström type has not been seen, the recent collections from St. Kitts appear to correspond accurately to the original description of Wikström, and suggest that many parts of Rydberg's description be discounted.

*Rubus ferrugineus* should be described as follows: Sterile shoots (primocanes?) delicate, long and trailing, sparsely strigose-pubescent becoming glabrate, cylindrical, purplish-brown in color. Leaves of sterile shoots with petioles 1.5–2 cm. long, leaflets 3, ovate-lanceolate, 4 × 1 to 5.5 × 3 cm. long and broad, the apex acuminate, the base obtuse or rounded, the margins sharply and finely serrate. Flowering canes arching, scrambling, slender and terete, strigose and non-glandular, pubescent becoming glabrate. Prickles numerous, scattered, recurved, broad-based and about 3 mm. long. Leaves 3-foliolate, the petioles 3–4 cm. long, strigose, conspicuously armed with short recurved prickles. Leaflet blades oblong-ovate, 5.5 × 3 to 8.5 × 3.4 cm. long and broad, the apex abruptly short acuminate, the base rounded or very slightly cordate, soft in texture

(neither coriaceous nor parchment like), glabrate above, variously pubescent below. Leaflets with 8–9 pairs of primary veins. Inflorescence a terminal panicle to 20 cm. long and 10 cm. in diameter, the rachis gray-tomentose and armed with short recurved prickles. Calyx lobes gray-tomentose on both surfaces, ovate in flower, becoming elongated to 1 cm. long in fruit. Stamens numerous with the outer ones abortive and conspicuous. Pistils gray-tomentose, forming mature achenes 3 mm. long, rugose.

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# THE GENERA OF RHIZOPHORACEAE AND COMBRETACEAE IN THE SOUTHEASTERN UNITED STATES [1]

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RHIZOPHORACEAE R. Brown in Flinders, Voy. Terra Austral. 2: 549. 1814, "Rhizophoreae."

(RED MANGROVE FAMILY)

Evergreen trees or shrubs of muddy tidal shores, brackish streams or lagoons [or tropical rain forests], often with conspicuous prop or knee roots. Leaves mostly opposite with large, leaflike, caducous stipules. Inflorescences cymose or racemose. Fruit [a dehiscent capsule or] an indehiscent, leathery berry, bearing the persistent calyx. Seeds 1 to many, viviparous in the genera of coastal mangroves. TYPE GENUS: *Rhizophora* L.

A family of about 16 genera and 120 species distributed throughout the tropical and subtropical regions of the world, generally between 25° N. and 25° S. Latitude. *Rhizophora* L., *Bruguiera* Lam., *Ceriops* Arn., and *Kandelia* W. & A., which are the primary components of much of the world's coastal mangrove swamps,[2] are usually thought of as representative

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. The treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued to the present paper. The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions apply primarily to the plants of this area, with supplementary information in brackets. References not seen by the author are marked with an asterisk.

The author is grateful for the helpful comments and suggestions of Dr. Wood and for the preserved materials of *Rhizophora*, *Laguncularia*, and *Conocarpus* supplied by Drs. Wood, R. B. Channell, H. H. Iltis, and P. B. Tomlinson, and Mr. David Seligson. The illustration, the work of Dorothy H. Marsh, was supervised by Dr. Wood.

[2] The strange appearance of the mangrove trees with their tangled masses of long prop roots extending down into the water has been recorded by travelers for centuries. Theophrastus (305 B.C.) wrote of mangroves in the Persian Gulf which were "eaten away up to the middle by the sea and are held up by their roots so that they look like a cuttlefish" (Theophrastus, *Enquiry Into Plants* [transl. A. Hort] 1: 343. 1916). An

of the family, but most of the genera are inhabitants of inland tropical rain forests. A single species, *Rhizophora Mangle* L., occurs in the southeastern United States.

Bentham and Hooker separated the four genera of mangroves from the rest of the family as tribe Rhizophoreae (leaves opposite, style one, endosperm scanty, and embryo macropodous). Wood structure of this tribe, also distinct from that of the inland genera, is characterized by scalariform intervascular pitting, heavy-barred scalariform perforation plates, scanty vasicentric parenchyma, multiseriate rays, and libriform fibers. In addition, only the coastal genera have prop roots and vivipary, apparent adaptations to the littoral habitat. Schimper ignored the morphological similarities among the genera of Rhizophoreae, believing them to be the result of parallel adaptations to the habitat, and related each genus to a different inland genus, a concept not generally accepted.

Embryologically, the genera of Rhizophoraceae differ in several respects from one another (see Mauritzon); each genus shares one or more characters with several different families in the Myrtales. The family is considered most closely related to the Combretaceae on the basis of the unilocular ovary and usually single-seeded fruit. Chromosome numbers of $2n = 36$ and 64 have been reported for the family.

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1. **Rhizophora** Linnaeus, Sp. Pl. 1: 443. 1753; Gen. Pl. ed. 5. 212. 1754.

Gregarious trees or shrubs inhabiting mud flats of coastal tidal marshes or shallow brackish streams and lagoons, bearing conspicuous, bowed prop roots at the base of the tree and other adventitious roots from the lower branches. Branching opposite, rarely alternate. Leaves petiolate, decussate, simple, entire margined, leathery, persistent, elliptic, oblong to obovate or lanceolate, punctate on the lower (abaxial) surface, stipulate; stipules interpetiolar, leaflike, convolute, surrounding the unexpanded leaf and falling as the leaf expands. Inflorescence axillary, cymose, dichotomously branched with 2–8[–16] flowers, or the flowers solitary, the pe-

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extensive account of *Rhizophora* in early literature may be found in Bowman (1917, pp. 592–603).

duncles and pedicels subtended by connate, 2–4-lobed bracteoles, the flowers borne among [or below] leaves of the current year. Flowers pedicellate [or sessile], regular, bisexual, 4-merous. Sepals 4 (5), ± distinct, valvate in aestivation, persistent, leathery, each with a prominent central longitudinal rib on the inner surface. Petals 4, distinct, alternate with the sepals and folded lengthwise in bud into the depression between the ribs of adjacent sepals, deciduous, leathery, white or yellowish white, lanceolate, equal to or shorter than the sepals, the margins densely villous [or glabrous]. Stamens 8[–12], in 1 whorl, the filaments short or wanting; anthers elongate-deltoid, apiculate, introrse, the inner (adaxial) sides filled with numerous areolae containing pollen and covered by a thin membrane, the apex and 2 longest sides of the membrane becoming free during pollen discharge; pollen oblate-spheroidal, tricolporate, the pores fused laterally forming a zone around the equator, the exine smooth to faintly scabrate, the greatest diameter of the grain about 18$\mu$. Gynoecium syncarpous, bicarpellate; stigmata punctate; style filiform and forked at the apex [or nearly wanting]; ovary 1, the upper portion solid, the 2(–4) locules inferior, each with 2 axile, anatropous ovules pendulous from the apex of the locule and surrounded by spongy tissue, the micropyle upward and outward. Fruit a conical, indehiscent, leathery berry, attached at the base to the receptacle. Seed 1, rarely 2, the other ovules abortive, the apparent placentation parietal due to displacement of the placenta and abortive ovules by the developing seed; seed coat thick, fleshy. Embryo straight, green, in the micropylar end of the endosperm, developing (without a dormant period) into the seedling while still within the fruit on the tree; hypocotyl pendulous, clavate, protruding from the fruit and ultimately disarticulating at the junction with the cotyledons; cotyledons thick, fused into a green tube, protruding from the fruit and withering with it after the seedling has fallen. Embryo sac development of the normal (Polygonum) type; endosperm development of the nuclear type. LECTOTYPE SPECIES: *R. Mangle* L., typified by removal of the remaining Linnaean species of *Rhizophora* to other genera of the Rhizophoraceae. (Name from Greek, *rhiza*, root, and *phoros*, bearing, in reference to the conspicuous prop roots.) — MANGROVE.

A pantropical genus of six to nine species in two sections, RHIZOPHORA and AËROPE Endl.; represented in the Americas by *Rhizophora racemosa* G. F. W. Mey., *R. Harrisonii* Leechman, and *R. Mangle* of sect. RHIZOPHORA (flowers borne among leaves produced the same year, peduncles as long as or longer than the petioles, flowers pedicellate, and stamens eight). Only *R. Mangle*, the red mangrove, a pioneer colonist of silted tidal shores, extends northward into our area to Levy County, on the west coast of Florida, and to Volusia County, on the east, with its greatest development along the low southwestern shore in the region of the Ten Thousand Islands. North of Volusia County the red mangrove does not survive severe winter frosts, and the mangrove swamp is replaced by

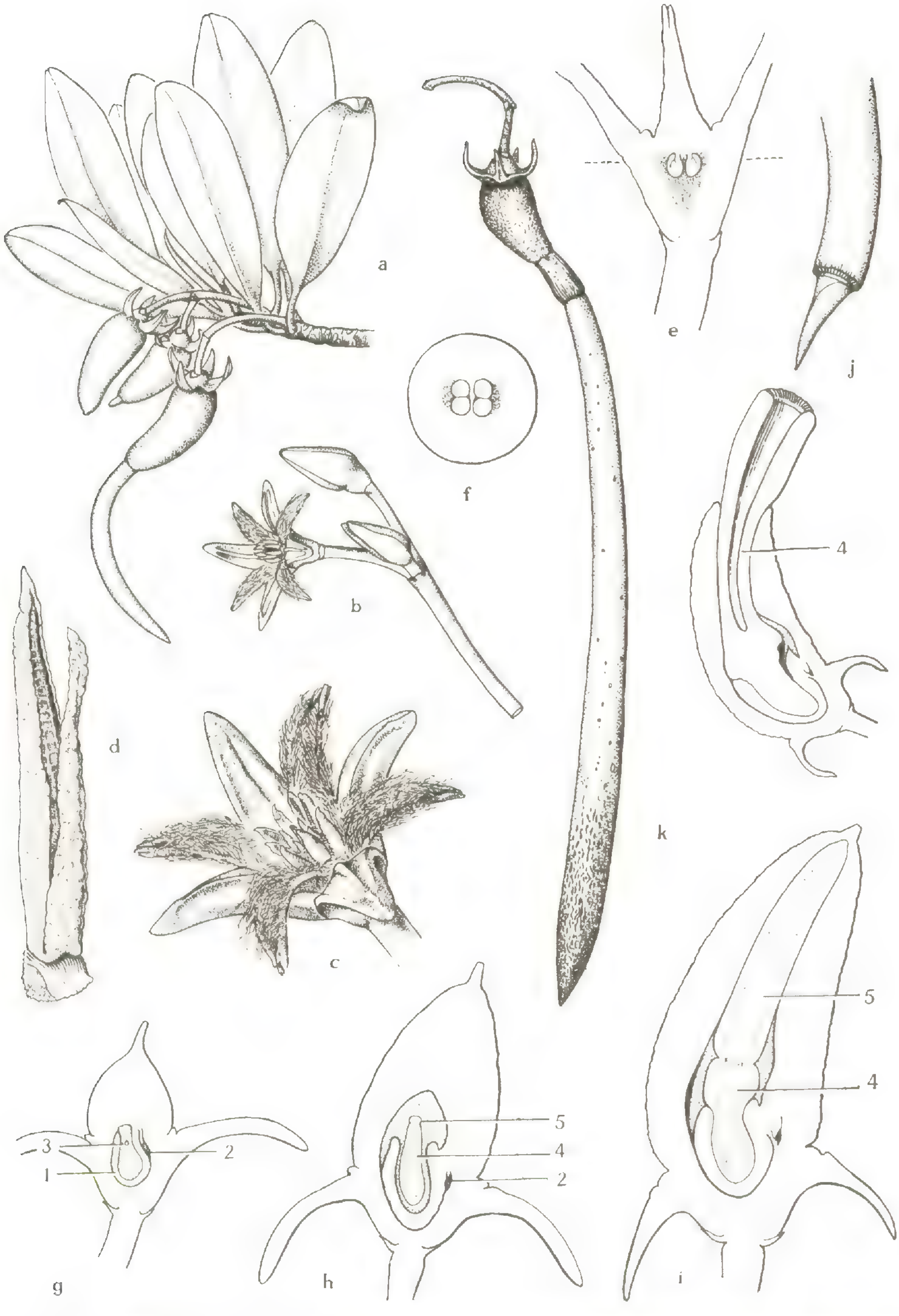


FIG. 1. **Rhizophora.** a–k, *R. Mangle*: a, fruiting branchlet, showing successive stages in development of hypocotyl, × 1/2; b, inflorescence, × 1; c, flower, × 2; d, stamen, inner view, showing mode of dehiscence and pollen areolae, × 16; e, gynoecium and calyx in diagrammatic vertical section, the pendulous ovules surrounded by spongy tissue, × 4; f, two-locular ovary in diagrammatic cross section at level of broken line in "e," × 4; g–j, enlarging fruit in semi-diagrammatic vertical section, showing progressive development from embryo to seedling, × 2 (except j, × 1) — note endosperm (stippled), 1-seed coat, 2-aborted ovule, 3-embryo, 4-cotyledons, 5-hypocotyl (in "j" hypocotyl disarticulated from the cotyledonary tube revealing plumule); k, fruit with seedling showing fully elongated cotyledonary tube and hypocotyl, × 1/2.

salt-marsh vegetation. The mangrove areas of Florida have been estimated to cover more than 1000 square miles (Davis).

The same species, *Rhizophora racemosa*, *R. Harrisonii*, and *R. Mangle*, also occur along the West African coast from Senegal to Angola. *Rhizophora racemosa*, infrequent in the Americas, is the dominant species along the African shore, while *R. Mangle*, the most widespread American species, is less abundant and restricted to dryer ground inland. According to Savory, *R. Mangle*, having a high salt tolerance, is confined in Africa to land which, during the dry season, is flooded only at high tide, so that salt accumulates by evaporation, and which, during the wet season, is not flooded by fresh river water in the delta areas. Differences in distribution of this species on the two continents are difficult to explain on the basis of present information. The species of *Rhizophora* on East African shores are of Indo-Malaysian affinity, the East and West African coasts sharing no species in common. Plants of *R. Mangle* from the Pacific coasts of North and South America and a few Pacific islands (e.g., Fiji, Samoa, Tonga, and New Caledonia) have slightly smaller flowers with shorter styles than those in the rest of the range and have been recognized by some authors as a distinct species, *R. samoënsis* (Hochr.) Salvoza. This distinction is questionable, with at least one character, length of styles, so variable as to make separation of the species on that character impossible (Hou, 1960). There are no positive records of hybrids within the genus.

Environmental factors determining the distribution of the red mangrove include type of soil, salinity of water and soil solutions, tides, water levels, and temperature. *Rhizophora* grows best in shallow water (with a salt concentration at least one-third that of sea water) on deep peat or marl soils free from violent wave action. Recent experiments with *R. Mangle* seedlings in various concentrations of salt solutions show that best development occurs with a salt concentration equalling that of sea water, although seedlings are apparently facultative to a wide range of salinity and are even capable of surviving in fresh water to a limited extent (Stern & Voigt). Plants growing naturally in waters with relatively low salt concentrations, as in parts of the Everglades, tend to be stunted or dwarfed. The high salinity of the water and soil in which *Rhizophora* grows suggested to Schimper that mangroves were physiologically xerophytic and, consequently, had a low rate of transpiration, a much-disputed conclusion. Recent studies indicate transpiration rates are indeed low, but more work is needed on this problem, as well as on all aspects of the physiology of *Rhizophora*.

In addition to *Rhizophora*, the name "mangrove" has been applied to several different genera in at least four other families. *Avicennia* (Verbenaceae), *Pelliciera* (Theaceae), *Sonneratia* (Sonneratiaceae), and *Laguncularia* and *Conocarpus* (Combretaceae) are all "mangroves," characterized by high salt tolerances and the ability to persist along heavily silted shores. The extensive tidal forests which they form are known as mangrove swamps. The swamp formation, an exceptionally uniform one

for the tropics, where diversity is the rule, is generally comprised of three or four genera of mangroves, either in mixed populations, or occupying particular zones in relation to the distance from the shore line. When zonation occurs, *Rhizophora* is in the outermost zone where the substrate is covered by water even at low tide. Other genera, such as *Avicennia* or *Laguncularia*, occur farther inland, where they are only partially flooded at high tide. The tidal action apparently promotes good aëration and gas exchange in the prop roots. Once established, mangrove swamps may play a minor role in accumulation of debris and silt leading to new land formation, but it is doubtful that they are of value in land reclamation, since accumulation of silt usually is not initiated by, but must precede, their establishment.

The red mangrove has both absorptive underground roots and aërial roots. Clusters of superficial, underground, secondary roots appear early in the seedling, taking over the function of the weakly developed taproot. These bear numerous absorptive rootlets, each with a small "rootcap" composed of cells adhering to the rootlet as it grows laterally outward from the parent root. Aërial roots, known as prop roots for their supposed stabilizing action in anchoring the plant to the substrate and generally most abundant on the offshore side ot the tree, form along the main stem of the young mangrove about the second year of growth. In older plants additional adventitious aërial roots may form along the lower branches. The surface of the aërial roots is supplied with lenticels which function in maintaining a high oxygen tension in the underground roots submerged in anaërobic mud.

The genera of mangroves in the Rhizophoraceae are notable for vivipary, the germination of the embryo in the seed while the fruit is still attached to the parent plant. In *Rhizophora* normally only one or rarely two ovules develop. Polyembryony is unknown. The growth of more than one hypocotyl from a fruit, implying the occurrence of polyembryony, is due to development of more than one ovule. As the embryo and endosperm grow, the nucellus and inner integument disintegrate, while the outer integument becomes very thick and fleshy, with much vascular tissue, purportedly for transport of nutrition to the embryo. The endosperm, composed of large, translucent cells, is abundant and during development of the embryo grows out of the micropyle, spreading over the outer integument to form an arillode. The presence of absorptive papillae on the endosperm has suggested that the endosperm functions as a placental organ rather than as reserve nutritional material (Bowman, 1917). The embryo develops directly into the seedling without a dormant period. The hypocotyl elongates, piercing through the seed coat and apex of the ovary wall, and is followed by the distal end of the cotyledons, which are fused into a green tube. (See FIG. 1, j.) The plumule lies in the hollow center of the cotyledonary tube. When the hypocotyl is fully elongated, an abscission layer forms at the junction of the hypocotyl and the cotyledons causing disarticulation of the two parts, the hypocotyl and plumule falling into the water or mud below, the cotyledons remaining attached

to the fruit and withering with it. From fertilization to the falling of the seedling is said to occupy nine to ten months. The hypocotyl at the time of fall averages about 25 cm. in length.

The question of how the seedlings become planted has been a controversial one. Early writers (and even many recent ones) believed the hypocotyls plunged vertically downward from the tree, like falling darts, into the mud below where they took root, but more recent observations show that the hypocotyl generally is unable to land erect in the mud because of its slight curvature. It is suggested that the hypocotyls upon falling float, first horizontally, later vertically, until stranded, then gradually become erect through strong upward curvature at the base just above the radicle. The seedlings may float for several months and can retain their vitality up to five months in a dry state, making them capable of being dispersed great distances (Guppy). Regeneration of roots and buds from short pieces of hypocotyl has been reported.

Stellate and H-shaped sclereids are present in practically all parts of the plant. The air-dried bark contains up to 40% tannin, but the tannin is of poor quality, imparting an undesirable red color to leather, and is not used extensively. Large mangrove trees are used in building, particularly as underwater pilings. Small trees are cut in many parts of the world for firewood, and the dense, hard wood is used in making charcoal. Fossil leaves from the Middle Eocene of Georgia, and a fossil calyx from the Lower Eocene of Tennessee have been described as possibly belonging to *Rhizophora*.

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COMBRETACEAE R. Brown, Prodr. Fl. Nov. Holland. 351. 1810, nom. cons.

(WHITE MANGROVE FAMILY)

Shrubs, trees [or woody climbers], mainly of tropical coasts. Buds naked (at least in our genera). Leaves evergreen or deciduous, entire, opposite, alternate, or spirally whorled in dense clusters at the ends of short branches, exstipulate, petiolate or sessile, the blade lanceolate, elliptic, or obovate, often with 2 glands at the base and numerous small pits (domatia) on the undersurface. Inflorescence an axillary spike, terminal panicle, or compact, globose head. Flowers regular [rarely slightly irregular], sessile, bisexual or both bisexual and ♂ in the same inflorescence, usually proterogynous, each subtended by a bract [or the bract absent]. Floral tube glabrous, hairy [or scaly], of 2 distinct parts [of 1 part in the West African *Strephonema*]; lower part adnate to the ovary, tubular or flattened laterally and ± 2-winged; upper part, above the ovary, deeply or shallowly cupuliform, persistent or deciduous; calyx lobes (4)5(6)-merous, deltoid, valvate or imbricate in the bud, hairy [or glabrous] within, sometimes scarcely developed. Petals none or 5 and distinct, greenish white, shorter [longer] than the calyx lobes, deciduous. Stamens 5–10, in 2 whorls, deciduous; filaments scarcely to well exserted; anthers orbicular or cordiform, versatile, 2-locular, longitudinally dehiscent. Gynoecium probably 1-carpellate; stigma capitate or punctiform; style filiform, free from [or adnate to] the upper part of the floral tube, generally surrounded at the base by a nectariferous disc; ovary inferior

[half-inferior in *Strephonema*], 1-locular; ovules 2(–6), anatropous, pendulous from the apex of the locule on slender, generally papillose funiculi. Fruits indehiscent, of various types (scalelike and imbricate in a cone-shaped head, or ellipsoid and laterally flattened, or fleshy and drupelike [or dry with 2–5 broad, papery wings]), composed predominantly of flotation tissue, sometimes also with a sclerenchymatous layer. Seed 1, the other ovules abortive; seed coat membranaceous to thick; endosperm of the nuclear type, scanty or none. Embryo large, straight, often green; cotyledons thick, fleshy, spirally convolute [or plicate]; radicle weakly developed, superior. (Terminaliaceae Jaume St.-Hil. Expos. Fam. 1: 178. *pl. 29*. 1805.) TYPE GENUS: *Combretum* Loefl., nom. cons. (*Grislea* L., 1753, nom. rejic.).

A pantropical family of about 18 genera and 450 species; the largest genera, *Combretum* (250 species) and *Terminalia* (200 species), best developed in the Old World Tropics. The classification of Engler & Diels, with two subfamilies and five tribes, is generally followed. Four genera in two of the four tribes of subfam. Combretoideae are represented in the Southeastern States in southern Florida or the Keys.

The Combretaceae are related to Rhizophoraceae and Myrtaceae and distinguished from them by the unilocular ovary with two to six ovules suspended from the apex of the locule by slender funiculi. The family is characterized anatomically by the common occurrence of intraxylary phloem in the stem, bicollateral veins in the leaves, and the presence at the base of the leaf blade of two flask-shaped cavities containing a multicellular gland. Transparent dots sometimes apparent in the leaves are due to large stellate idioblasts in the mesophyll which contain calcium oxalate crystals. Curious unicellular hairs containing a conical or concave membrane which makes them appear bicellular are widely distributed in the family (cf. Cistaceae). The fruits of practically all genera are well adapted to dispersal by water by virtue of their thick aërenchymatous mesocarp and the ability to float several months in sea water without adverse effect on germination (Guppy). The seed is protected in many genera by a stony endocarp.

Most species are believed to be insect pollinated. The main independent evolutionary tendencies in the family, according to Exell (1954), are elongation of the upper part of the floral tube, leading to pollination by long-tongued insects; congestion of small flowers into spikes or racemes, accompanied by reduction in size of petals; and development of winged fruits, allowing for dispersal by air. Fossil leaves thought to represent *Combretum*, *Conocarpus*, *Laguncularia*, and *Terminalia* are known from the Eocene (Claiborne flora) of Alabama, Mississippi, and Georgia. In addition, a fossil pollen grain of an unknown genus of the Combretaceae has been recorded from the same flora, and a fossil flower related to *Combretum* has been collected from Eocene beds of Tennessee.

Timbers of several species of *Terminalia* are of local importance in construction, and *Bucida* and *Laguncularia* are also used to a limited

extent in the West Indies for building. A tea made from the roasted leaves of *Combretum sundaicum* Miq., a jungle climber native to Malaya, is believed to combat craving for opium. Another climber, *Quisqualis indica* L., Rangoon creeper, $2n = 22, 24$, is cultivated in warm regions for its attractive rose or red tubular flowers. Chromosome numbers of $2n = 22, 24, 26$, and 36 are reported in the family.

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## KEY TO THE GENERA OF COMBRETACEAE

General characters: *leaves with 2 inconspicuous glands at the base of the blade; flowers regular, the floral tube mostly of 2 parts, the lower part generally tubular and adnate to the ovary, the upper part cupuliform; ovary inferior, 1-locular; ovules pendulous on slender funiculi; fruit indehiscent, 1-seeded.*

A. Leaves spirally whorled in terminal clusters on short branchlets; fruits ovoid or obliquely ovoid, not conspicuously flattened or winged; petals none; inflorescence racemose; bracteoles on floral tube lacking.
  B. Fruit fleshy, drupelike, ovoid, 20–70 mm. long; calyx lobes well developed, deltoid, deciduous from apex of fruit. ..... 1. *Terminalia*.
  B. Fruit dry and leathery, obliquely ovoid, 5–10 mm. long; calyx lobes scarcely developed, persistent at apex of fruit. ..... 2. *Bucida*.

A. Leaves alternate or opposite, not clustered; fruits scalelike or obovoid, laterally flattened, 2-winged.
  C. Leaves alternate; fruits scalelike, imbricate in a cone-shaped cluster; bracteoles on the floral tube none; petals none. ..... 3. *Conocarpus*.
  C. Leaves opposite; fruits obovoid, solitary; bracteoles on the floral tube 2; petals 5. ..... 4. *Laguncularia*.

### Subfam. COMBRETOIDEAE

### Tribe TERMINALIEAE DC.

1. **Terminalia** Linnaeus, Syst. Nat. ed. 12. **2**: 674 (err. 638). 1767; Mant. Pl. 21, 128. 1767, nom. cons.

Trees [rarely shrubs], often with sympodial branching. Leaves deciduous, large, glabrous or with sparse reddish-brown hairs, the apex acute to acuminate, the blade minutely verruculose [rarely with canal-like mucilage cavities] and with 2 inconspicuous glands at the base. Inflorescence a densely flowered axillary spike [rarely a terminal or axillary panicle]. Flowers bisexual or both bisexual and ♂ with the ♂ flowers on the terminal part of the spike, the bisexual flowers on the basal part of the spike, [4]5-merous, subtended by an ovate bract [or bract wanting], both flowers and bracts with dense reddish-brown pubescence. Floral tube greenish white, the lower part narrowly tubular, the upper part shallow, broadly cupuliform, deciduous; calyx lobes [4] 5 [6], deltoid, valvate in bud, densely silky haired within at the base [or glabrous]. Petals wanting. Stamens [8] 10 [12]; filaments exserted; anthers orbicular. Stigma punctiform. Style surrounded at the base by a thickened

5[4 or 6]-lobed disc, the disc densely covered with silky reddish-brown hairs [or glabrous]; ovules 2 (3 or 4). Fruit fleshy and drupelike, ovoid, apiculate at the apex; pericarp of several layers: a fleshy outer one, a fibrous one, a spongy one often containing air cavities, and an irregularly shaped sclerenchymatous inner one, often with pockets of aërenchyma [or the fruit dry, membranaceous, 2–5-winged]. Seed coat thin. (*Adamaram* Adans., 1763, and *Panel* Adans., 1763, nom. rejic.) TYPE SPECIES: *T. Catappa* L. (Name from Latin, *terminalis*, terminal, referring to the leaves clustered at the ends of the branchlets.)

A complex pantropical genus of about 200 species in 20 sections; represented in our area by *Terminalia Catappa* L., Indian almond, $2n = 24$, of sect. TERMINALIA (§ *Eucatappa* Engl. & Diels), in which the fruit is compressed but lacks wings. Native to Polynesia, *T. Catappa* has become naturalized in scattered areas of southern Florida and the Keys. It is widely planted in the tropics as a shade tree, and the young trees, particularly, are admired for their regular, tiered manner of branching. Finger-like growths at the base of the petioles have been interpreted as rudimentary stipules which are drawn inward to an axillary position as the blade of the leaf grows. The seed is edible and is said to have a filbert-like flavor. Its size varies widely, the cultivated races generally having larger fruits than the wild trees (Exell, 1954). The fruits, containing 30–35% tannic acid, find limited use in tanning.

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2. **Bucida** Linnaeus, Syst. Nat. ed. 10. 1025, 1368. 1759, nom. cons.

Trees of tropical coastal hammocks, the young growth clothed with silky reddish-brown hairs; branching sympodial. Leaves evergreen, petiolate [or sessile], obovate to elliptical, mostly without glands at the base of the blade, arranged in spiral whorls in dense clusters at the ends of

branchlets, the branchlets subtended by 2 short spines or without spines. Inflorescence a densely flowered axillary spike [rarely pseudo-umbellate]. Flowers bisexual, 5-merous, subtended by an ovate bract, both flowers and bracts with dense reddish-brown pubescence. Floral tube greenish, the lower part tubular, the upper part shallowly cupuliform, persistent; calyx lobes 5, scarcely developed, valvate in bud, hairy within. Petals wanting. Stamens 10; filaments exserted; anthers cordiform. Stigma punctiform. Style surrounded at the base by a thickened disc. Fruit obliquely obpyriform, not winged or ribbed, the apex bearing the persistent upper part of the floral tube; pericarp composed of a leathery outer layer and a central stony layer with spongy aërenchyma on both sides. Seed coat thin. (*Buceras* P. Br., 1756, nom. rejic.) TYPE SPECIES: *B. Buceras* L. (Name from Latin, *bucida* or *bucaeda*, one who is beaten by a whip made of ox hide; application of the name obscure.)

A tropical American genus of three or four species, with one, *Bucida Buceras*, black-olive, widely distributed from Panama to southern Mexico and in the West Indies, extending northward to Elliott's Key in the Florida Keys.

The genus is very similar to, and perhaps derived from, *Terminalia*, with which it has been united by several authors. The two are easily distinguished in the New World by the difference in the shape and internal structure of the fruit. Exell (1958), although maintaining both genera, has indicated that the distinctive distinguishing fruit characters are lacking in one or two Malayan-Polynesian species of *Terminalia*, which, however, appear unrelated to *Bucida* in any other features. A re-evaluation of the taxonomic relationship of the two genera is desirable, but should be preceded by a comprehensive study of *Terminalia*, a large and morphologically diverse genus which has never been monographed.

In *Bucida Buceras* the fruits are occasionally invaded by a gall-forming mite (*Eriophyes* sp.). The fruits become much elongated, up to 16 cm., and curved or twisted. The name *Buceras*, horn of an ox, is derived from the resemblance of the galls to such horns. Spines derived from lateral buds are present on some plants of this species. Rudimentary stipules, similar to those in *Terminalia Catappa*, have also been reported.

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3. **Conocarpus** Linnaeus, Sp. Pl. 1: 176. 1753; Gen. Pl. ed. 5. 81. 1754.

Shrubs or trees of sandy coasts and hammocks marginal to mangrove swamps [or of borders of tropical rivers], with erect to prostrate, glabrous to densely silver-haired stems. Leaves evergreen, alternate, shortly petio-

late or sessile, the blade elliptic, ovate [or narrowly lanceolate], the apex acute to acuminate or apiculate, the base with 2 raised glands, the lower (abaxial) side with several small pits (domatia), each at the juncture of the midvein with a secondary vein and occasionally also along the outer margin. Inflorescence a globose, many-flowered, conelike head, sessile or pedunculate. Flowers bisexual or both bisexual and ♂ in the same inflorescence, 5-merous, subtended by an ovate, concave bract, the apex of the bract acuminate. Floral tube greenish white, the lower part laterally flattened and 2-winged, the upper part cupuliform, deciduous; calyx lobes 5, valvate in bud, velutinous within. Petals wanting. Stamens 5–8(–10), well exserted, deciduous; anthers orbicular. Stigma punctiform. Style surrounded at the base by a fleshy, velutinous disc. Fruits leathery, laterally flattened, 2-winged, scalelike, imbricate in a conelike cluster; pericarp of thin, leathery outer and inner layers with spongy aërenchyma between. Seed coat thin. LECTOTYPE SPECIES: *C. erectus* L.; typified by the union of the two original species under *C. erectus* by De Candolle, Prodr. 3: 16. 1828. (Name from Greek, *konos*, cone, and *karpos*, fruit, in reference to the conelike head of fruits.)

A genus of two species, *Conocarpus erectus*, the buttonwood, of tropical America and West Africa, and *C. lancifolius* Engl., known only from the river valleys of the northern Somaliland highlands of East Africa. *Conocarpus erectus* reaches northward into Florida as far as Hernando County, on the west coast, and Merritt Island (Brevard County), on the east, occurring inland from the mangrove swamps on ground generally free from inundation by high tides. The alternate, elliptical leaves and fruits clustered into globose, conelike heads are characteristic. It fruits abundantly, but only an estimated 3–10% of the fruits contain seeds (Guppy). The cause of low seed set has not been determined.

The species shows a wide variation in stature and pubescence. Plants range in form from prostrate shrubs in rocky habitats to erect trees on sandy hammocks. The low-growing plants have been recognized by some authors as var. *procumbens* DC. A second, var. *sericeus* DC., has been recognized for plants with silver-haired pubescence which occur in the northern part of the species range. The common glabrous form and the densely pubescent extreme occur mixed in the same population. Both are without distinct geographical range and probably should be regarded only as minor variants. The wood of *C. erectus* is very hard, burning slowly like charcoal, and is prized as a fuel in the West Indies.

REFERENCES:

Under family references see BRANDIS, EXELL (1931, 1954), GUPPY (pp. 201–204), SARGENT, STEARN, and THORNE.

CHIOVENDA, E. Flora Somala. xvi + 436 pp. *50 pls.* Rome. 1929. [*C. lancifolius*, 173.]

HARSHBERGER, J. W. The comparative leaf structure of the sand dune plants of Bermuda. Proc. Am. Philos. Soc. **47**: 97–110. *pls. 1–3.* 1908. [Includes *C. erectus*.]

LAESSLE, A. M., & C. H. WHARTON. Northern extensions in recorded ranges of plants on Seahorse and associated keys, Levy County, Florida. Quart. Jour. Fla. Acad. Sci. **22:** 105–113. 1959. [*C. erectus*, 110, 111; seed dispersal mainly by sea currents.]

LITTLE, E. L. Miscellaneous notes on nomenclature of United States trees. Am. Midl. Nat. **33:** 495–513. 1945. [*C. erectus*, 507, 508.]

RUSSELL, A. *Conocarpus erecta* (buttonwood, Zaragoza-mangrove), a new domestic source of tannin. Chemurg. Dig. **2:** 27–29. 1943.*

Tribe LAGUNCULARIEAE Engl. & Diels

4. **Laguncularia** Gaertner f. Fruct. Sem. Pl. 3: 209. *pl. 217.* 1805.[3]

Shrubs or trees of coastal mangrove swamps and hammocks, often with small, pencil-like pneumatophores. Leaves evergreen, opposite, leathery, glabrous, oblong to obovate with the apex generally obtuse or retuse, shortly petiolate with 2 glands on the petiole at the base of the blade, the blade with numerous submarginal pits (domatia?) at the ends of the secondary veins. Inflorescence of terminal panicles, or solitary spikes in the axils of leaves. Flowers greenish white, fragrant, bisexual, 5-merous, subtended by a deciduous bract. Floral tube cupuliform to tubular, fleshy, scarcely produced beyond the ovary, inconspicuously ribbed, accrescent, silvery pubescent to glabrous, bearing 2 ovate bracteoles at the apex beneath the calyx lobes; calyx lobes 5, broadly deltoid, imbricate in bud, persistent. Petals 5. Stamens 10; filaments scarcely exserted; anthers orbicular. Stigma capitate. Style surrounded at the base by a thick, flattened disc. Ovules suspended on very short funiculi. Fruit ellipsoid to mostly obovoid, laterally flattened, with 2 thick, spongy wings, densely silvery haired to glabrous, bearing the persistent calyx at the apex; pericarp of leathery outer and inner layers with spongy aërenchyma between. Seed coat thick. TYPE SPECIES: *L. racemosa* (L.) Gaertn. f. (Name from Latin, *laguncularis*, flask- or bottle-shaped, in reference to the shape of the fruit.) — WHITE MANGROVE.

A monotypic genus of the American and West African coastal mangrove swamps. *Laguncularia racemosa*, with opposite leaves, flowers with five small petals, and conspicuous sessile, gray, flask-shaped fruits has a range practically identical with that of the red mangrove, *Rhizophora Mangle*. Where mangrove swamps occur in the Gulf of Mexico region, *Laguncularia* is found growing either mixed with *R. Mangle* and *Avicennia germinans*

[3] *Laguncularia* has been equated, by some authors, with the earlier genus *Horau* Adans. (Fam. Pl. 2: 80. 1763), but, according to Adanson's description, *Horau* has terminal, solitary flowers with no petals, four stamens, and an ovoid, capsular fruit containing a stony seed, characters which do not apply to *Laguncularia*. In addition, Adanson reports that camels browse the leaves of *Horau*, an unlikely fate for an American-West African genus of mangrove swamps. The name *Horau* was taken by Adanson from Kaempfer, who applied it to an East Indian coastal plant with alternate leaves. On this evidence it appears that *Laguncularia* and *Horau* are not synonymous and that *Laguncularia* is in no danger of displacement.

(L.) L. (the black mangrove of the Verbenaceae) or in a distinct zone inland between these genera and *Conocarpus erectus*. It seems to grow best on land at least partly flooded by salt or brackish water at high tide. In Florida, *Laguncularia* occurs as far north as Hernando County, on the west, and Merritt Island (Brevard County), on the east coast.

As with other genera of the family, few observations have been made on the biology of *Laguncularia*. It is known to be semiviviparous, the green embryo generally only piercing the seed coat while in the fruit on the tree, and germination generally not proceeding further until the fruit has fallen. No studies have been made on the origin of the floral tube in Combretaceae, but in *Laguncularia* (and the Old World *Lumnitzera* and *Macropteranthes*) bracteoles present on the tube suggest the possibility that it is partly cauline in origin. The wood of the white mangrove is used extensively in Puerto Rico for fence posts. Attempts are being made there to control cutting and production of *Laguncularia*, so it may become a profitable economic crop.

REFERENCES:

Under family references see BRANDIS, EXELL (1931, 1958), GUPPY (pp. 221–223), SARGENT, STEARN, and THORNE.

SCHENCK, H. Ueber die Luftwurzeln von *Avicennia tomentosa* und *Laguncularia racemosa*. Flora **72**: 83–88. *1 pl.* 1889. [Anatomy and brief discussion of function of pneumatophores.]

WADSWORTH, F. H. Growth and regeneration of white mangrove in Puerto Rico. Carib. Forester **20**: 59–71. 1959.

# THE GENUS CHAENOMELES (ROSACEAE) *

CLAUDE WEBER

## TAXONOMY

**Chaenomeles** Lindley, Trans. Linn. Soc. **13**: 96. 1822, as "*Chaenomeles*."
TYPE SPECIES: *Chaenomeles japonica* (Thunb.) Lindl. ex Spach.

*Pseudochaenomeles* Carrière, Revue Hort. **1882**: 238. *f. 52–55*. 1882.

Deciduous or half-evergreen shrubs with spiny branches and smooth bark. Buds small, glabrescent, with conduplicate vernation. Leaves alternate on young shoots, alternate or fasciculate on old wood, subsessile, simple, ovate, serrate, or crenate, with glands (or foliar nectaries) terminating and between the teeth, reticulate, glabrous or pubescent beneath when young, becoming glabrescent. Stipules reniform, free, occurring on young shoots only; leaves on old wood exstipulate. Flowers axillary, very numerous, solitary, or more often fasciculate, appearing on old wood and before the leaves in the spring, on leafy shoots in the summer and fall. Bracts caducous, subulate in spring inflorescences, subulate or reniform in summer inflorescences. Flowers regular, hermaphrodite, or male by abortion of styles and/or ovules (more rarely female by abortion of stamens). Calyx tubular-campanulate, 5-lobed. Sepals 5, imbricate in aestivation, short, entire, obtuse, often irregular in length, glabrous on the outer surface, ciliate but not glandular, pubescent within, erect at blooming time, usually caducous. Petals 5, large, free and unguiculate, inserted in the throat of the hypanthium, pubescent at base, red or pink, less often white, with veins no darker than the rest of the petal, caducous before wilting. Stamens 40–60, arranged more or less in two rows, filaments free, red or white (depending on the season), anthers inserted below the petals, introrse, innate to slightly versatile when mature, bilocular, yellow. Pollen grains tricolpate, smooth. Disc small, nectariferous, covering the carpels which are fused on their abaxial side to the hypanthium. Carpels 5, completely fused in a 5-celled ovary containing numerous anatropous ovules arranged horizontally in 2 rows in each locule. Placentation axile. Styles 5, connate at the base or up to ½ their length, glabrous or pubescent at base, ¼ longer than the stamens. The column formed by the fused styles sometimes persistent and becoming the umbilicus of the umbilicate fruits. Stigmata discoid or more often decurrent, extending on the styles following the junction of the edges. Fruit a short-stalked pome formed of the hypanthium, the flesh with grit cells, the carpels becoming cartilaginous. Seeds ovoid, numerous in each of the 5 locules,

* Continued from volume XLV, p. 205.

pointed at one end, testa coriaceous and dark brown, raphe and chalaza apical, endosperm lacking. Germination epigeal.

VERNACULAR NAMES. English: Japanese Quince, Flowering Quince, Japonica. French: Cognassier du Japon, Poirier du Japon. German: Japanishe Quitte. Japanese: Boke.

USES: Ornamental shrubs cultivated for their abundant and early flowers which appear before the leaves. Numerous spines render the plants useful for hedges. The easily forced flowers are sold as cut flowers during the winter. The fruits are used in jelly and preserves. Leroi (1924) recommends double cooking to eliminate the strong and acid taste. Used in France in a liqueur called *cydonade* (Burvenich, 1900), and in the preparation of *ratafia* (Morren, 1851).

In China the fruits (mostly in a dried state) are used medicinally in treating cramps, cholera, beriberi, stomach and intestinal pains, rheumatism, sunstroke, and as a sedative and excitant. The active principles are malic, tartaric and citric acids, and vitamin C (Loh, 1954).

DISTRIBUTION. China, Tibet, Bhutan, Burma, Japan. Cultivated in Asia, New Zealand, Australia, Europe, Africa and North and South America.

Kaempfer (1712), the first European to have seen a Japanese Quince, described it under the name of "Buke," a misspelling for the Japanese name "Boke."

Thunberg (1784) described *Pyrus japonica*, based on a specimen he had collected which is still preserved at the Växtbiologiska Institutionen at Uppsala (UPSV). This species became the basis for the genus described by Lindley (1822) as *Chaenomeles* (from the Greek *chaino*, to gape, and *melon*, apple). Although Thunberg's type specimen consisted of flowering material only, he described fruit of his new species in a manner which has since been shown to be incorrect. He wrote "Pomum subglobosum, glabrum, magnitudine iuglandis, 5-valve, 5-loculare." Except for the expression "5-valve" the description is accurate. There is no explanation why Thunberg thought the fruit was dehiscent; although the pome shrivels and dries, it never opens.

In describing the genus *Chaenomeles* Lindley wrote, "The fruit is only known from Thunberg's description who says it splits into five valves." His detailed description was, "*Choenomeles*. Pyri species Thunb. Willd. Cal. campanulatus, 5 dentatus, carnosus. Stamina erecta, serie duplici inserta. Pomum quinquevalve, polyspermum. Frutex (Japoniae). Folia lucida, coriacea, crenata. Flores terminales, coccinei."

In 1825 DeCandolle treated *Chaenomeles* as a section of *Cydonia* and pointed out the error of Thunberg when he stated, "Thunberg asserit pomum 5-valve, sed vereor ne descr. sit erronea."

In spite of some confusion concerning the characters of its fruit, the genus *Chaenomeles* is distinct and homogeneous, and may be recognized

easily by a series of characters among which are the following: reniform stipules; short erect, entire, glabrous sepals; stamens in two rows; and numerous seeds.

In 1875, Carrière wrote that on the basis of the figures given in the Gardeners' Chronicle, *Pyrus maulei*, described by Masters in 1874, should be placed in *Chaenomeles* rather than in *Pyrus*; but he did not make the transfer. In 1876 he published an article with numerous figures illustrating the variation found in the fruits of the other species of *Chaenomeles* then commonly cultivated, *C. speciosa*. When later he saw fruits of the plant at that time called *Pyrus maulei*, he found them sufficiently different to justify the creation of a subgenus *Pseudo-Chaenomeles*. Accordingly, although he considered the taxon a subgenus, he treated the combination simply as *Pseudo-Chaenomeles maulei*. Neither Carrière nor any later botanist used this combination again. It seems to me that the species of *Chaenomeles* are so very closely related that there is no need of subgeneric categories.

It should be noted in considering specific characters that herbarium specimens of *Chaenomeles* are rarely complete. The flowers usually appear before the leaves and are of no use in identifying the species, being on the one hand very much alike in the whole genus, and on the other hand offering a range of variation on the same shrub, according to the season. Although botanists are reluctant to collect sterile specimens, these are, in *Chaenomeles*, often more useful than fertile ones. Very distinctive specific characters, found in the serration and the type of pubescence of the leaves, are of great use in determination of hybrids. The confusion between the three species of *Chaenomeles* and the two of *Cydonia* could have been completely avoided by using the distinguishing characters of the adult leaves.

In this monograph the genus *Chaenomeles* is treated as including three species, *C. japonica* (Thunb.) Lindl. ex Spach, *C. speciosa* (Sweet) Nakai, and *C. cathayensis* (Hemsley) Schneider. As stated in my earlier paper (1963), hybrids have been developed between these species in every mathematical combination. The Superba group consists of hybrids between *C. japonica* and *C. speciosa*; the first cultivars appeared after 1890 as chance seedlings in different nurseries. In 1921 a cross was made by Philippe de Vilmorin of Verrières-le-Buisson, France, by pollinating flowers of *C. speciosa* with pollen of *C. cathayensis*, producing 'Vedrariensis,' the first cultivar of the Vilmoriniana group. Walter Clarke of San Jose, California, crossed *C. cathayensis* with *C. japonica* producing a group of seedlings from which he selected the first two cultivars of the Clarkiana group in 1945. Earlier, in 1938, he had crossed successfully *C. cathayensis* with *C.* × *superba* to produce cultivars which are a synthesis of the three species, and which form the Californica group.

## Key to the Species and Hybrid Groups of Chaenomeles

A. Leaves crenate; shrubs not more than 1.5 m. high; branches spreading or

erect-spreading, with slender spines; fruits small, to 4 cm., ripening early in the season.

B. Leaves regularly crenate, always glabrous; second year twigs [9] heavily verruculose; flowers salmon-orange (rarely white); fruits apple-shaped. ..... 1. *C. japonica.*

B. Leaves irregularly crenate, some partially serrate, glabrous, or when young with pubescent veins on the under surface; second year twigs sparsely to moderately verruculose; flowers white, pink, orange, or red; fruits apple-shaped. ..... 4. *C.* × *superba.*

A. Leaves sharply serrate (rarely subentire); shrubs 1.2–3 m. high; branches very erect or erect-spreading, with spines or spurs; fruits medium or large, ripening later in season.

C. Leaves serrate, serrations terminating in a short, sharp tip; branches first erect then spreading, with spines.

D. Second year twigs glabrous; leaves finely serrate, when young with glabrous or pubescent veins on the under surface; flowers red, white, or pink. ..... 2. *C. speciosa.*

D. Second year twigs sparsely verruculose; leaves coarsely serrate, glabrous, or when young with a light fulvous tomentum on the under surface; flowers pink. ..... 5. *C.* × *clarkiana.*

C. Leaves serrate (rarely subentire), serrations terminating in an awn-like tip; branches stiff and erect, with spines or spurs.

E. Adult shrubs normally 1.8 m. high; second year twigs sparsely verruculose; flowers pink or rosy-red, or both; fruits medium to large, ovoid or apple-shaped, normally less than 8 cm. long; seeds not flattened on both sides, ovoid. ..... 7. *C.* × *californica.*

E. Adult shrubs 2–2.4 m. high or higher; second year twigs completely glabrous; flowers white to pink; fruits large, more than 8 cm. long; seeds flattened on both sides.

F. Shrubs 2–2.4 m. high; branches numerous, erect-ascending, with spines or spurs; leaves when young with a light fulvous tomentum on the under surface; fruits approximately 8 cm. long. ..... 6. *C.* × *vilmoriniana.*

F. Shrubs 3 m. high; branches few, straight-erect, with spurs only; leaves glabrous, or when young covered by a thick fulvous tomentum on the under surface; fruits usually 15–20 cm. long. ..... 3. *C. cathayensis.*

1. **Chaenomeles japonica** (Thunb.) Lindl. ex Spach, Hist. Nat. Vég. Phan. 2: 159. 1834, as to name, not as to descr.

Var. **japonica**

*Pyrus japonica* Thunb. Fl. Jap. 207. 1784. Holotype, Japan, *Thunberg* (UPSV).
*Malus japonica* (Thunb.) Andrews, Bot. Repos. 7: *pl. 462.* 1807, as to name, excl. text and plate.
*Cydonia japonica* (Thunb.) Persoon, Syn. Pl. 2: 40. 1807.
*Cydonia japonica* var. α *typica* Makino, Bot. Mag. Tokyo 22: 63. 1908.

[9] The second-year twigs are exstipulate and located at the base of the new shoots which possess reniform stipules. The warts are absent on the older branches because of the shedding of the epidermis after the second year.

*Pyrus maulei* Masters, Gard. Chron. II. 1: 757. *f. 159.* 1874. Holotype. ex horto Maule, Bristol, England, April 1874, *Masters* (K).
*Cydonia maulei* (Masters) Moore, Florist & Pomologist **1875**: 49. *pl.* 1875.
*Chaenomeles japonica* var. *maulei* (Masters) Lavallée, Arb. Segrez. 110. 1877.
*Pyrus japonica* var. *maulei* (Masters) Burvenich, Revue Hort. Belge **26**: 241. 1900.
*Chaenomeles maulei* (Masters) Lavallée in Beissner *et al.*, Handb. Laubh.-Benenn. 182. 1903.
*Chaenomeles alpina* Koehne, Deutsche Dendr. **1893**: 262. 1893.

Dwarf bushy shrubs about 0.6–1.2 m. high; the widely spreading branches with short slender spines. Young shoots covered with a short scabrous tomentum; second year shoots verruculose. Leaves obovate to spathulate, (3–) 4–5 cm. long (petiole included), (1–) 2–3 cm. broad, coarsely crenate, short petioled, glabrous even when young (rarely with a few trichomes on the midrib of the under surface); stipules reniform, crenate, 1 cm. long, 1.5–2 cm. broad. Spring flowers on old wood very abundant, in clusters of (1–) 2–3 (4–). Open flowers cup-shaped to flat, 3–4 cm. broad. Sepals green to purple (depending on the amount of light). Petals salmon-pink to orange-red. Stamens 40–60. Styles 5, fused at the base in a column, glabrous all their length; stigmata green. Pomes the shape of gnarled apples, yellow, blotched with red (if sufficient heat), about 4 cm. in diameter, weighing up to 30 grams, skin slightly viscid. Seeds numerous, ovoid, pointed at one end, reddish-brown, shiny, to 80 (usually less) in one fruit, 6–8 mm. long, 4–5 mm. broad.

Flowering from March to June, depending on the latitude or altitude; also with a few flowers during the rest of the year in favorable weather.

VERNACULAR NAMES. Chinese: Cha-tzu, Mu-T'ae. English: Dwarf Japanese Quince. French: Cognassier du Japon, Poirier du Japon. German: Japanische Zierquitte, Japanische Birne. Japanese: Boke, Kusa-boke, No-boke, Ko-boke, Shidomi, Shidome, Jinashi or Dzinashi, Chiku-ume.

USES. The same as for the genus; less often cultivated than *C. speciosa*. *C. japonica* is hardier than the other species of *Chaenomeles* probably because of its dwarfness, its flower buds being protected under the snow. Its fruits require less heat than those of the other two species to ripen and show coloration.

DISTRIBUTION. Hillsides, river and lake banks, Japan; from 300 to 7000 feet.

**Japan.** Honshū (Hondo). Miyagi pref., Siogama, May 8, 1909 (G). Tochigi pref., Nikko, *Sargent*, Sept. 2, 1892 (A), *Rev. Père Faurie*, May 27, 1898 (K). Gumma pref., Fujioka in Shimotsuke, *Ohwi*, Apr. 21, 1951 (A, G, K, L, NY, US).

UPSV). Nagano pref., Mt. Togakushi, July 10, 1884 (TI); Prov. Shinano, foot of Mt. Yatsu-gatake, about 1600 m., *Furuse*, May 24, 1954 (A). Tokyo pref., Tokyo, *Matsumura*, March 30, 1879 (US); Minamitama, *Suzuki*, Apr. 14, 1951 (A); Prov. Musashi, Arai, Apr. 21, 1911 (US); Honsyn, *Yamazaki*, Apr. 13, 1947 (AAH). Fuchu-Tamamura, *Mishushima 914*, March 21, 1951 (A). Kanagawa pref., Kamakura, *Wilson 6616* (A), *Momiyama 722* (TI); Yokohama, *Maximowicz*, 1862 (BM, L, NY, P). Yamanashi pref., Prov. Kai, near Kasukabe, *Wilson 6332* (A), Yatsuga-d-ake, *Wilson 7527* (A), Shiwotsu, *Nakai*, (TI), Mt. Howo, *Matsuda*, May 25, 1954 (TI). Shizuoka pref., Yokosuka (as Yokoska), *Challenger Exp.*, Apr. & May, 1875 (K); Numazu, *Lyle*, May, 1908 (BM); foot of Mt. Fuji, *Adachi*, June 10, 1934 (TI), *Satake*, May 26, 1935 (TI); slope of Mt. Fuji, 1500–3000 ft., *Wilson 6656* (A); Fuji, *Tuyama*, July 14, 1934 (TI); Mt. Fuji, *Kanai*, May 18, 1937 (TI). Gifu pref., Prov. Mino, *Shiota 1070* (A), *1071* & *5009* (A). Kyūshū. Nagasaki pref., Nagasaki, *Oldham*, 1862 (K, L).

ALSO RECORDED: Honshū. Okayama pref., Prov. Bitchiu, Koidzumi (1913). Shikokū. Koidzumi (1913). Kiūshū. Oita pref., Prov. Bungo. Kagoshima pref., Prov. Osumi, Koidzumi (1913).

CULTIVATED: Japan, Sweden, Poland, Germany, Netherlands, England, United States. Also: China, Forbes & Hemsley (1887); New Zealand, Harrison (1959); Australia, Hurley (1948) and Lord (1948); Romania; Finland; Switzerland; Italy; France.

**Japan.** Hokkaido. Hakodate (prob. cult.), *Comm. Perry's exped.*, 1854 (NY), *Dr. Albrecht*, 1861–63 (GH). Honshū. Amori pref., Mirosaki, prob. cult., *Faurie 6695* (AAH, BM). Yamanashi pref., Kasukabe Exp. Sta. Med. Pl., Kasukabe-shi, *Kawatani*, Apr. 10, 1961 (AAH).

**Sweden.** Uppsala Bot. Trädgård, *Juel*, June 1, 1925 (UPSV); Skåne, Alnarp, July 1, 1881 (UPSV).

**Poland.** Silesia, Wroclaw (formerly Breslau, Germany), Schneitniger Park, *Baenitz*, May 8 & July 21, 1905 (AAH, G, GH, L, US).

**Germany.** Göttingen, Landn. Inst., *Rehder 615* (AAH).

**Netherlands.** Bot. Gard. Arb., Wageningen, *Steenbergen & Prehn 50* (AAH); Schiedam, *Vervoort*, Apr. 22, 1939 (L).

**United States.** U. S. Dept. Agr., Washington, D.C., *Vasey*, 1878 (US); Biltmore, N.C., *Biltmore Herb. 5716* (US); Huntington Bot. Gard., Calif., *Walther 280 & 281* (AAH).

CULTIVARS of *Chaenomeles japonica*

'Arthur Hill', Morton Arb. (cult. under Illinois, no. 7), Lisle, Illinois, *Weber*, May 24, 1962 (AAH).

'Aurea', Arnold Arb. no. 654–50, Jamaica Plain, Mass., *Weber*, May 17, 1962 (AAH).

'Dorothy Rowe' (formerly 'Pygmaea Alba'), Stanley M. Rowe Arb., Cincinnati, Ohio, *Weber*, Apr. 27, 1962 (AAH).

'Dwarf Poppy Red', Belmonte Arb. no. 139–49, Wageningen, Neth., *Steenbergen & Prehn*, Apr. 4, 1961 (AAH).

'Maulei', Kew Gard., Engl., type specimen illustrated in Bot. Mag. as *tab. 6780*, Sept. 22, 1883 (K); Univ. of Washington Arb. no. 2397–41, Seattle, Wash., *Witt*, Apr. 22, 1961 (AAH).

'Orange Beauty', Proefst., Boskoop, Neth., *Roberts*, Apr. 14 & June 27, 1961 (AAH).
'Pigmani', Arnold Arb. no. 496–59, Weston, Mass., *Weber*, May 11, 1962 (AAH).
'Plena', Yokohama, Japan, *Iwata* 5550 (Herb. Iwata, Yokohama, Jap., not seen).
'Sargentii', Proefst., Boskoop, Neth., *Roberts*, Apr. 14 & June 27, 1961 (AAH); Arnold Arb. no. 3680 (from Sargent's seed), Jamaica Plain, Mass., *Rehder*, May 3, 1921 (AAH).
'Taiojishi', Morton Arb. no. 258–39, Lisle, Ill., *Schulenberg*, May 15, 1961 (AAH).
'Tricolor', Arnold Arb. no. 2538, Jamaica Plain, Mass., May 11 & Oct. 2, 1889 (AAH).

CULTIVAR represented by an illustration:

'Zoge' (formerly 'Alba'), *Iwasaki*, Honzu Dzufu 60, fol. 10 recto, *pl. 1919*.

When Thunberg described his *Pyrus japonica* in 1784 the plant had not yet been introduced into cultivation in Europe and the species was represented only by the type specimen in Uppsala.[10]

In 1796, Sir Joseph Banks, then director of the Royal Botanic Gardens, Kew, introduced into England a Flowering Quince from Japan which was erroneously thought by Sims (1803) to be *Pyrus japonica* Thunb. For this reason the specific epithet "japonica" was incorrectly applied to the species now known as *Chaenomeles speciosa* (Sweet) Nakai, for almost a century.

Andrews (1807) perpetuated the error. He thought that Thunberg's plant was a *Malus* and illustrated as *Malus japonica* (Thunb.) Andr. the plant here treated as *Chaenomeles speciosa*. Lindley and Spach also were unaware of the identity of *Chaenomeles japonica* although they were responsible for the nomenclatural combination. As a result, the names of these several authors are nomenclatural synonyms of *Chaenomeles japonica*, although taxonomically referable to *C. speciosa*.

According to Moore (1875), the first opportunity for European botanists and horticulturists to see true *Pyrus japonica* Thunb. was in Bath, England, in June 1873 "when a drawing of the plant, with samples of the conserve made from its fruit, was shown under the name of a Japanese species of *Crataegus* or *Pyrus*, and received a First-Class Certificate."

In the spring of 1874 flowering specimens for description and illustration were sent to the Gardeners' Chronicle. Masters (1874a), knowing only the so-called *Chaenomeles japonica* which was actually *C. speciosa*, decided that the material sent in was different, and described it as *Pyrus maulei*, named for the Messrs. Maule, who had introduced it in 1869. It was not until autumn of the same year (1874b) that Masters completed his description of the fruit of the species. *Pyrus maulei* was introduced into the United States by the U.S. Department of Agriculture

[10] This type specimen consists of two flowering branches in a poor condition, the flowers having been attacked by insects. The specimen does not have any data, but Thunberg in the description says "in Monte Fakona," now Mt. Hakone, in Honshū, Kanagawa prefecture.

soon after its introduction into Europe. The differences between the two species, *Chaenomeles japonica* and *C. speciosa*, were not quickly recognized, nor was acceptance of the generic name *Chaenomeles* widespread, factors accounting in part for much of the nomenclatural confusion and the large number of synonyms.

Maximowicz, who collected during many trips to Japan, increased the number of taxa in the genus as well as the nomenclatural confusion (Maximowicz, 1873). In assigning three varieties to *Chaenomeles japonica*, the identity of which he had misinterpreted, he created a taxonomic problem which was not clarified for many years. His *Chaenomeles japonica* var. *α genuina* is not equivalent to var. *japonica* of this treatment but is rather a synonym of *C. speciosa*, a species to be considered later. His varieties *β alpina* and *γ pygmaea*, on the other hand, are maintained as varieties of *Chaenomeles japonica* as defined in this monograph.

Some material previously called *Chaenomeles japonica* var. *alpina* in the United States, or *C. sargentii* Lemoine in Europe, was material cultivated from seed collected on the mountains of Honshū Island, Japan, by Sargent in 1892. As the shrubs from this material grown at the Arnold Arboretum did not maintain their distinctiveness, Sargent did not continue to call them var. *alpina*. They differ somewhat from material introduced by the Messrs. Maule from plains in Japan, in being more dwarf and having lighter fruit production. Material from Sargent's seed is a strain here called *Chaenomeles japonica* 'Sargentii', while that from the Maule introduction is *C. japonica* 'Maulei'.

Makino (1908) may be credited with clarifying the identity of Thunberg's plant. He said it corresponded to *Cydonia japonica* var. *α typica* Makino, while the plant grown in Europe for over a century, which unfortunately he believed conspecific, should be called *Cydonia japonica* var. *β lagenaria* cultivated in Japan as introduced from China.

Koidzumi (1913) treated the entire genus *Chaenomeles* and cited characters (serration of leaves, warting of twigs, etc.) by which the species may be recognized. In 1909, he had returned var. *β lagenaria* of Makino to specific rank and assigned it to the genus *Chaenomeles*, as *Chaenomeles lagenaria* (Loisel.) Koidz. (now *C. speciosa*). This left free the specific epithet "japonica" for what is *Pyrus japonica* Thunberg. In 1913, the name *Chaenomeles japonica* was, for the first time, applied to the proper taxon.

In cultivation *Chaenomeles japonica* usually blooms later than *C. speciosa*, and its leaves develop at nearly the same time as the flowers. The late blooming insures better pollination and higher fruit production. *C. japonica* is more often reproduced by seeds. It shows little variation in the color of the flowers, differing mostly in the intensity of an orange shade, and in their size. Nevertheless, among the multitude of seedlings raised in Japan, Europe, and in America, some forms with white or double flowers, variegated foliage, etc., have been selected and are now

reproduced asexually. These are represented by the cultivars enumerated below.

Var. **alpina** Maxim., Bull. Acad. Sci. St.-Pétersb. **19**: 168. 1873. Syntypes, Japan, mountains of Kujus-San (as Kundsho-san), Nagasaki, *Maximowicz*, 1863 (GH, K, L); mountains of the interior of Kyūshū, *Maximowicz*, 1862 (BM).

Smaller in all its parts, and more branched than either var. *japonica* or var. *pygmaea*. Flowers in May.

DISTRIBUTION. Rocky slopes of the mountains of the island of Kyūshū, Japan, in Oita and Nagasaki prefectures. Only type material was examined.

When Maximowicz (1873) described var. *alpina*, he compared it with var. *genuina*, now *C. speciosa*, and said it was different in being more ramified, smaller in all its parts, and with truncate leaves. The four herbarium specimens collected by Maximowicz, which consist of fragments of flowering branches, with male flowers only, show this variety to be smaller than *C. japonica* var. *japonica*. Truncate leaves which are extremely frequent in the typical variety, and occur on specimens of var. *pygmaea*, should not be considered characteristic.

Var. *alpina* Maxim. is a dubious variety which should not be put in synonymy of the type species until more authentic material, especially of adult leaves, has been examined. The plants cultivated under this name and reported to revert to the type did not originate in the Island of Kyūshū. It is not known whether or not this variety has a disjunct distribution with var. *japonica*. Both occur on the Island of Kyūshū and the herbarium labels, as well as the literature, do not give any information about the altitude at which either of them is found. The mountain Kujus-San on Kyūshū reaches an altitude of 5866 ft. The varieties *japonica* and *alpina* are possibly the two extremes of a cline found from sea level to mountain heights. More material is needed to determine whether they are ecotypes or deserve varietal rank.

Var. **pygmaea** Maximowicz, Bull. Acad. Sci. St.-Pétersb. **19**: 168. 1873. Isotypes, Japan, Yokohama, *Maximowicz*, Dec. 1862 (GH, K, NY).

Trunk subterranean, branches spineless or nearly so. Flowers from December to April.

DISTRIBUTION: Thickets, grassy banks of the basal region around Tokyo and Yokohama.

**Japan.** Honshū. Tokyo pref., Tokyo, *Miyabe*, March 29, 1882 (A), s. coll., May 1887 (US), *Wilson*, Apr. 17, 1910 (A); Prov. Musashi, s. coll., Apr. 1884 (G), Tizuka, *Watanabe*, Apr. 12, 1891 (GH). Honsyn, *Yamazaki 2526* (A). Kanagawa pref., Yokohama, syntypes.

In 1873, when Maximowicz described var. *pygmaea*, he stated that it grows near Yokohama "cum *a*." which is now considered by all authors to represent *C. speciosa*, found only cultivated as var. *genuina*. On one sheet in the Gray Herbarium are specimens collected and annotated by Maximowicz as *Pyrus japonica* var. *pygmaea*, from Yokohama, Dec. 1862, and *Pyrus* (*Cydonia*) *japonica* Thunberg, from Yokohama, 1862. Between his second trip to Japan, and the description of these specimens, Maximowicz changed from using *Pyrus* to *Chaenomeles*. From the Maximowicz specimen of *Pyrus japonica* (now *Chaenomeles japonica* var. *japonica*), var. *pygmaea* differs in its subterranean branches, shown by the presence of adventive roots, its smaller size (but larger than var. *alpina*), and its spineless condition. The syntypes consist of a few small, straight fragments of flowering branches. The dried flowers are up to 3.5 cm. broad, about twice as large as the flowers of var. *alpina*. In his description, Maximowicz said that the pedicels are three times as long as the calyx. This is not the case on his original material, and the pedicel length is known in this genus to vary according to the temperature. From the length of the pedicels, and the size of the flowers they appear to be late summer flowers, or at least flowers without an interruption in the vegetative period. In this case, the leaves are much smaller than, although similar in appearance to, adult leaves of var. *japonica*.

The branch of var. *japonica* collected by Maximowicz near Yokohama, probably at the same time as the specimens of var. *pygmaea*, is 50 cm. long, spiny, and in fruiting condition. Subsequent material referable to var. *pygmaea* was collected in flower in March and April, not December and January, as Maximowicz says in the description. Without more material and data, it is impossible to decide if var. *pygmaea* and var. *japonica* which are sympatric are isolated by flowering time, or are only part of the normal variation expected in a population. In cultivation *Chaenomeles japonica* is noted for its spreading branches, which root so easily that the plant is often increased in gardens by layering.

As far as we know, no authentic material of var. *pygmaea* has ever been introduced into cultivation in Europe or America. The plants grown under this name represent different strains of var. *japonica*. The only way to settle definitely the question of varietal rank in *Chaenomeles japonica* would be by growing side by side, plants of the three varieties, from cuttings as well as from seeds, to check whether they revert to a common type.

2. **Chaenomeles speciosa** (Sweet) Nakai, Jap. Jour. Bot. **4**: 331. 1929.

*Cydonia speciosa* Sweet, Hort. Suburb. Lond. 113. 1818. Holotype, plate no. *692* (not 629), Bot. Mag. **18:** 1803.

*Cydonia lagenaria* Loiseleur in Duhamel, Traité Arb., Arbust. (Nouv. Duhamel) **6:** *255, pl. 76.* 1815.

*Cydonia japonica* var. *β lagenaria* (Loisel.) Makino, Bot. Mag. Tokyo 22: 64. 1908.

*Chaenomeles lagenaria* (Loisel.) Koidzumi, Bot. Mag. Tokyo **23**: 173. 1909.

*Chaenomeles japonica* var. *α genuina* Maximowicz, Bull. Acad. Sci. St.-Pétersb. **19**: 168. 1873.
*Cydonia japonica* var. *genuina* (Maxim.) Ito, Bot. Mag. Tokyo **14**: 117. 1900.
*Chaenomeles angustifolia* Koidzumi, Jour. Coll. Sci. Tokyo 34, art. **2**: 97. 1913.
*Chaenomeles eugenioides* Koidzumi, Bot. Mag. Tokyo **29**: 160. 1915.
*Chaenomeles trichogyna* Nakai, Fl. Sylv. Kor. **6**: 42, *pl. 15*. 1916. Holotype, Mt. Chiisan, Korea, *Nakai*, 1915? (TI).
*Chaenomeles cardinalis* Nakai, Jap. Jour. Bot. **4**: 333, 1929.
*Chaenomeles eburnea* Nakai, *ibid.* 330.
*Chaenomeles extus-coccinea* Nakai, *ibid.*

Shrubs dense, usually 2 m. high, occasionally up to 5 m. (especially against a wall), with numerous branches, erect-spreading, spiny. Young shoots glabrous or slightly pubescent; the second year ones glabrous. Leaves ovate to oblong, glabrous or when young slightly pubescent on the veins of the under surface, sharply serrate, short petioled, 4.5–10 cm. long, 2–4 cm. broad; stipules reniform, serrate, 0.5–1 cm. long, 1.2–2 cm. broad. Spring flowers on old wood, very abundant, in clusters of (1) 2–6, with short pedicels, before the leaves. Open flowers cup-shaped, 4–5 (6) cm. broad. Sepals green to purple, depending on the amount of light. Petals usually red, but also white or pink (similar variation among wild specimens). Stamens 40–60. Styles 5, fused at the base in a column; entirely glabrous or slightly hairy to woolly on the fused portion; stigmata green. Pomes very variable, most often apple-shaped, also pear-shaped or ovoid, often umbilicate, skin dry, 4–7 cm. long, 3–6 cm. broad, weighing up to 100 grams (usually less). Seeds numerous, ovoid, pointed at one end, brown, dull, up to 100 in one fruit, usually less, 6–8 mm. long, 4–5 mm. broad. Blooming from February to June, depending on the latitude or altitude, but also with a few flowers from January to December, weather permitting.

VERNACULAR NAMES. Chinese, Tieh kio hai tang, T'ich keng hait'ang, Hay-tan taoua, Hung mei; English, Japanese Quince, Flowering Quince, Japonica; French, Cognassier du Japon, Poirier du Japon, Cognassier à fruit en gourde; German, Japanische Quitte, Prächtige Quitte; Italian, Cotogno del Giappone; Japanese, Kara-boke, Hiboke, Kai dan boke, Ki buki, Yodo-boke.

USES. Same as for the genus, but more often cultivated than the other two species.

DISTRIBUTION. Hillsides, open thickets, rocky slopes, ravines, forests; China, from 600 to 5500 ft.; Tibet, and Burma.

**China.** Shensi. Shensi meridional, *R. P. David*, March 1874 (P). Kansu. Eastern Kansu, Tsingchow, *Hers 2409* (A). Szechwan. Between Pai kuo wan and Moso ying, *Schneider 624* (A). Kweichow. Pinfa, Kweiting, *Tsiang 5352*

(A, NY). Yunnan. Meng-tsze, *Henry 10730* (NY, US); Helungtan near Likiang City, *Feng 365* (A); Likiang Valley, *Feng 672* (A); Lu-se, *Tsai 56441* (A); vicinity of Yun-Nan-Sen, *Maire 1703* (K); Wen-shan Hsien, *Tsai 51501* (A); Swelf River, near Tengyueh, *Rock 7952* (A, US), *Rock 7990* (A).

**Tibet.** Kiala, Ta-tsien-Lou, *Soulié 701* (K, P).

**Burma.** Minekha ywa, Wa State, *Maung Po Khant 15300* (K); Myitkyina, lukpyi, *Kermode* 17101 (K).

CULTIVATED. China, Korea, Japan, Java, Australia, South Africa, Russia, Sweden, Norway, Poland, Germany, Austria, Switzerland, France, Belgium, Netherlands, England, United States. Also: Ryukyu, Ishigaki Isl. of the Yaeyama Archipelago, Nakai (1929); New Zealand, Harrison (1959); Egypt, Bircher (1960); Kenya, from 5500 ft. up, Blake (1950); Romania; Italy, Savi (1818); Belgium, Planchon (1849); Ireland, Loudon (1838); Canada; Argentina, Schleimer (1951).

**China.** Hopei (Chihli). China borealis, *Bunge*, 1837 (P); Peking *Bretschneider 282* (K), Prince Park, *Wang 26* (AAH). Shantung. Meng Shan, Fei Hsein (prob. cult.), *Cheo & Yen 137* (A, BM, G, P); Tsing-tao, First Park, *Chiao 2456* (A, NY, US); Chi Pan Shih, Lao Shan, *Chiao 2757* (AAH, G, NY, US). Kiangsu. Chinkiang, *Chiao 10507* (AAH); Nanking, Univ. Garden, *Ching 5103* (AAH). Chekiang. Tien Tai Shan, *Chiao 14434* (AAH); Tihtaishan, *Ching 1537* (AAH, US). Hupeh. Changyang, *Henry 5249* (AAH, K), *Wilson 129*, Apr. 7, 1900 (AAH, NY); Ichang, *Wilson 129*, March 3, 1900 (K), *Wilson 2990* (A, BM, GH, US). Kiangsi. Kiangtiang Mts. (prob. cult.), *Faber 923* (K). Hunan. Yang-Shan, Changning Hsien (prob. cult.), *Fan & Li 287* (A). Yunnan. Yunguing, *Schneider 3477* (G); valley behind Kin-tchong-chan, *Maire*, March 1912 (G); valley of Tong-Tchouan (prob. cult.), *Maire 217* (A); Shun-Ning Hsien (prob. cult.), *Wang 71957* (A), *Wang 72007* (A); Chen-Kang Hsien, *Wang 72259* (AAH), *Chang 72466* (A); Shunning (prob. cult.), *Yü 16053* (A); Puchitze, Likiang Valley, *Ching 20088* (AAH). Also: Kwantung. Yu-Ping Hsien, Feng-Hwang Shan, Chun (1940). Shensi. Shensi merid. Franchet (1883).

**Korea.** *Warburg 6399* (AAH); Seoul, Tun Kwan, Taikul, Apr. 24, 1895 (BM, K); Mt. Zokurisan, *Nakai*, Aug. 13, 1936 (TI).

**Japan.** Hokkaido. Hakodate (Kakodadi), *Wright*, 1853–56 (NY, US). Honshū. (Hondo). Aomori pref., Aomori plain, *Père Faurie 147* (K). Tochigi pref., Lake Chūsenji (Chuzinji), *Wilson 6803* (AAH). Tokyo pref., Tokyo, *Myabe*, 1880 (AAH), *Wilson 6340* (AAH, BM, GH, US), *Wilson 6341* (AAH, US), *Wilson 6365, 6366, 6367* (AAH, US), *Terakawa 74* (US). Kanagawa pref., near Yokohama, *Bisset 1071* (BM). Shizuoka pref., Mt. Hakone (Fakone), *Bremitted 974* (L); Prov. Idzu, *Furuse*, Apr. 5, 1958 (AAH). Hyogo pref., Himeji, naturalized, *Fujita*, 1937 (TI). Kyūshū, Nagasaki pref., Nagasaki, *Oldham*, 1862 (K, P); Kagoshima pref., Kase Gawa (naturalized ?), *807* (L). Tanega Shima, *Wilson 6136* (AAH). Yakushima, *Wilson 6099* (AAH).

**Java.** *Blume* (L).

**Australia.** Sydney Bot. Gard., *Boorman*, Sept., 1921 (AAH).

**South Africa.** Pretoria, Princes Park, *Reptin 13 B* (GH).

**Russia.** Leningrad (St. Petersburg), Bot. Gard., *K. A. Meyer*, 1832 (LE); Prov. Don, Margaritovka, Rostof reg., *Sarandinaki*, Apr. 29, 1906 (LE); Crimea, Urzuf Gard., *Von-Graf 95* (LE); Ukraine, Moldavia, Milety, *Gusev 216* (LE), Ismail, *Gusev*, June 9, 1955 (LE).

**Sweden.** Uppsala, Bot. Gard. *Trödg.*, 1853 (UPSV); Kalmar, *Dusén*, July 24, 1890 (UPSV), *Dusén*, June 4, 1892 (UPSV), *Dusén*, June 10, 1897; Malmö, *Johanson*, May 1887 (BM).

**Norway.** Oslo (Christiania), Bot. Gard., *Trödg.*, (UPSV).

**Poland.** Silesia, Walbrzych (formerly Waldenburg, Germ.), *Selsmann*, May 23, 1881 (L); Wroclaw (formerly Breslau, Germ.), Villa Lauterbach in Stabelwitz, *Lauterbach & Baenitz*, May 14 & July 20, 1908 (LE, US), Schneitniger Park, *Baenitz 249* (AAH, G, GH, L, LE, US).

**Germany.** Berlin, Bot. Gard., 1858 (LE), May 1, 1874, May 29, 1874, May 20, 1875 (LE); Thuringia, *Sagorski*, May 1898 (AAH).

**Austria.** Wien, Bot. Gard., *Schneider*, Apr. 24, 1901 (AAH).

**Switzerland.** Geneva, Apr. 27, 1864 (G).

**France.** Paris, Cels greenhouse, *Hardy*, March 24, 1817 (LE), Luxembourg Gard., *Gay*, August 5, 1822 (K); Paris ?, *Decaisne*, 1870, 1871 (P).

**Netherlands.** Poelgeesi, *6469* (L).

**England.** Cambridge, Bot. Gard., Apr. 1826 (LE), 1849 (GH); Sunninghill, *Parker*, Oct. 30, 1903 (AAH); Surrey, Coopers Hill, *Parker*, June 1904 (AAH).

**United States.** Massachusetts, Hyannis, escaped to roadside, *Fernald, Butters & St. John 15190* (GH); Brookline, Sargent's Gard., *Sargent*, May 14, 1888 (AAH). New Jersey, Watchung, *Moldenke 1465* (AAH). Pennsylvania, Philadelphia, Morris Arb. no. 1749, *Weber*, June 19, 1961 (AAH). District of Columbia, near Washington, *Ward*, Apr. 23, 1877 (US), Washington Bot. Gard., *A.L.S.*, Apr. 24, 1885, (US). Virginia, Boyce, Orland E. White Arb., *Wagenknecht 5315* (AAH). Ohio, Mentor, Holden Arb., *Lipp*, May 1, 1961 (AAH). Indiana, Tremont, *Bennett*, May 8 & June 27, 1954 (G). Illinois, Geneseo, *Harper*, July 19, 1898 (AAH). Missouri, St. Louis, Bot. Gard., *Kellog*, Apr. 24, 1906 (AAH). California, San Marino, Huntington Bot. Gard., *Walther 279* (AAH); Berkeley, Blake Gard., *Bracelin 1782, 2276, 2689* (L).

### CULTIVARS of *Chaenomeles speciosa*

'Alarm', Harrison Nurs., Palmerston N., N.Z., *Harrison*, Apr. 1961 (AAH).

'Alba Cincta', Highland Park no. 525, Rochester, N.Y., *Harkness*, May 15, 1961 (AAH).

'Alba Floribunda', Kew Gard., Engl., *Weber*, June 7, 1960 (AAH).

'Alba Grandiflora Plena', Arnold Arb. no. 51-61, Jamaica Plain, Mass., *Weber*, June 6, 1961 & Oct. 1, 1962 (AAH).

'Alba Picta', Arnold Arb. no. 5098, Jamaica Plain, Mass., May 24, 1914 (AAH).

'Alba Rosea', Highland Park no. 535, Rochester, N.Y., *Harkness*, May 15, 1951 (AAH).

'Angustifolia', Bot. Gard., Tokyo, Japan, *Koidzumi*, Apr. 1910 (TI).

'Apple Blossom', Arnold Arb. no. 22394, Jamaica Plain, Mass., *Weber*, May 6, 1960, Apr. 27 & May 7, 1962 (AAH).

'Atrococcinea', Arnold Arb. no. 176–40, Jamaica Plain, Mass., *Weber*, May 17, 1961 (AAH).

'Aurora', Proefst., Boskoop, Neth., *Roberts*, Apr. 5 & June 27, 1961 (AAH).

'Baltzii', Arnold Arb. no. 3058–2 = 13015, Jamaica Plain, Mass., May 23, 1914 (AAH).

'Blood Red', Arnold Arb. no. 195–42, Jamaica Plain, Mass., *Weber*, May 23 & Sept. 21, 1960 (AAH).

'Bonfire', Arnold Arb. no. 196–42, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Brilliant', Proefst., Boskoop, Neth., *Roberts*, Apr. 5 & June 27, 1961 (AAH).
'Candicans', Arnold Arb. no. 281–61, Jamaica Plain, Mass., *Weber*, May 24, 1962 (AAH).
'Candida', Arnold Arb. no. 197–42, Jamaica Plain, Mass., *Weber*, May 11 & May 23, 1960 (AAH).
'Candidissima' ("flore albo"), Geneva, Switz., *Deprèz*, Sept. 27, 1825 (NY); ("albiflora") Wroclaw (formerly Breslau, Germ.), Poland, Villa Lauterbach in Stabelwitz, *Lauterbach & Baenitz 1518* (AAH, GH, L).
'Cardinalis', Arnold Arb. no. 3175–1 = 13016, Jamaica Plain, Mass., May 24, 1914 (AAH).
'Contorta', Arnold Arb. no. 126–42, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
'Deep Pink', Arnold Arb. no. 389–50, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).
'Doctor Bang's Pink', Michigan State Univ., East Lansing, Mich., *Parmelee*, spring 1962 (AAH).
'Dwarf Red', Cranborne Manor, Cranborne, Engl., *Lady Cranborne*, 1961 (AAH).
'Echo', Univ. of Illinois, Urbana, Ill., *Kemmerer*, May 4, 1962 (AAH).
'Euphrosyne', Kew Gard., no. 58.47, Engl., *Weber*, June 7, 1960 (AAH).
'Eximia', Arnold Arb. no. 179–40, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
'Falconnet Charlet', Proefst., Boskoop, Neth., *Roberts*, Apr. 14 & June 27, 1961 (AAH).
'Fireball' (formerly 'Boule de Feu'), Planting Fields, Oyster Bay, N.Y., May 1962 (AAH).
'Flore Roseo' ("floribus roseis"), Japan, *Siebold* (L).
'Flore Rubro Aurantiaca', Leningrad (St. Petersburg) Bot. Gard., *70.5* (LE).
'Gaujardii', Arnold Arb. no. 601–52, Jamaica Plain, Mass., *Weber*, May 11, 1960 (AAH).
'Grandiflora', Arnold Arb. no. 2534–2 = 13018, Jamaica Plain, Mass, May 24, 1914 (AAH).
'Hanazono', Morton Arb. no. 240–39, Lisle, Ill., *Schulenberg*, May 15, 1961 (AAH).
'Japanese Scarlet', Arnold Arb. no. 201–42, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).
'Jimmy's Choice', James Kelley Nurs., New Canaan, Conn., *Kelley*, May 19, 1961 (AAH).
'Kermesina Semiplena', Arnold Arb. no. 5112, Jamaica Plain, Mass., May 24, 1914 (AAH).
'Knap Hill Radiance', Tudor House, Ripley, Engl., *Chadbund*, Sept. 1962 (AAH).
'Leonard's Velvety', Arnold Arb. no. 22393, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).
'Limoni', U.S. Nat. Arb. no. 1321, Washington, D.C., *Weber*, June 19, 1961 (AAH).
'Lutea Viridis', Kew Gard., Engl., *Weber*, June 7, 1960 (AAH).
'Macrocarpa', Arnold Arb. no. 3054–1 = 13019, Jamaica Plain, Mass., *Rehder*, May 3, 1921 (AAH).
'Mallarot', Arnold Arb. no. 53–61, Jamaica Plain, Mass., Weber, May 7, 1962 (AAH).
'Marmorata', Arnold Arb. no. 3048–1 = 13020, Jamaica Plain, Mass., May 24, 1914 (AAH).

'Moerloosei', Arnold Arb. no. 13021, Jamaica Plain, Mass., *Weber*, May 11 & May 23, 1960 (AAH).
'Nivalis', Veitch Nurs., Coombe Wood, Engl., *Nicholson*, March 1884 (K).
'Nivea Extus Coccinea' ("Extus Coccinea"), Exp. Sta. Med. Pl., Kasukabe-Shi, Japan, *Kawatani*, Apr. 10, 1961 (AAH).
'Pacific Red', Dawes Arb., Newark, Ohio, *Sanford*, May 1961 (AAH).
'Papeleui', Highland Park no. 523, Rochester, N.Y., *Harkness*, May 15, 1961 (AAH).
'Phylis Moore', Kew Gard. no. 171, Engl., Apr. 27, 1962 (AAH).
'Red Ruffles', Mount Airy Arb., Cincinnati, Ohio, *Weber*, May 22, 1962 (AAH).
'Red Sprite', Univ. of Illinois, Urbana, Ill., *Kemmerer*, May 4, 1962 (AAH).
'Rosea Grandiflora', Arnold Arb. no. 5109, Jamaica Plain, Mass., *Weber*, May 7, 1962 (AAH).
'Rosea Plena', Arnold Arb. no. 3055–1 = 13023, Jamaica Plain, Mass., May 24, 1914 (AAH).
'Rosea Semiplena', Arnold Arb. no. 5099, Jamaica Plain, Mass., *Rehder*, May 3, 1921 (AAH).
'Rubra', Morton Arb., Lisle, Ill., *Schulenberg*, spring 1962 (AAH).
'Rubra Grandiflora', Kew Gard. no. 408. 71, Engl., *Weber*, June 7, 1960 (AAH).
'Russell's Red', Tudor House, Ripley, Engl., *Chadbund*, Sept. 1962 (AAH).
'Sanguinea Plena', Highland Park. no. 522, Rochester, N.Y., *Harkness*, May 15, 1961 (AAH).
'Sanguinea Semiplena', Arnold Arb. no. 3051–1 = 13024, Jamaica Plain, Mass., May 23, 1914 (AAH).
'Shirataum', Villa Taranto, Verbania-Pallanza, Italy, *Platt*, Apr. 1961 (AAH).
'Simonii', Arnold Arb. no. 5111, Jamaica Plain, Mass., May 23, 1914 (AAH).
'Snow', Arnold Arb. no. 217–49, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
'Snow Queen', Hillier Nurs., Winchester, Engl., *Hillier*, Oct. 1962 (AAH).
'Spitfire', Arnold Arb. no. 662–50, Jamaica Plain, Mass., *Weber*, May 6 & 23, 1960 (AAH).
'Starlight', Univ. of Illinois, Urbana, Ill., *Kemmerer*, May 4, 1962 (AAH).
'Sulphurea Perfecta', Highland Park no. 539, Rochester, N.Y., *Harkness*, May 15, 1961 (AAH).
'Taioh-Nishiki' ('Taroyishi'), Arnold Arb. no. 974–62, Jamaica Plain, Mass., *Weber*, Sept. 19 & Oct. 2, 1962 (AAH).
'Tani-no-Yuki', Morton Arb. no. 259–39, Lisle, Ill., *Schulenberg*, May 15, 1961 (AAH).
'Texas Pink,' Morton Arb. no. 616–58, Lisle, Ill., *Schulenberg*, May 9, 1962 (AAH).
'Toyo-Nishiki', Morton Arb. no. 699–42, Lisle, Ill., *Schulenberg*, May 15, 1961 (AAH).
'Umbilicata', Arnold Arb. no. 855–53, Weston, Mass., *Weber*, May 17, 1961 (AAH).
'Versicolor', Arnold Arb. no. 3056–1 = 13025, Jamaica Plain, Mass., May 23, 1914 (AAH).
'Versicolor Lutescens', Arnold Arb. no. 13026, Jamaica Plain, Mass., *Kobuski & Metcalf*, May 9, 1930 (AAH).

Sir Joseph Banks, director of Kew Gardens, is usually credited for the introduction of *Chaenomeles speciosa* into Europe in 1796. From

England, it was brought to France by Mr. Boursault in 1810 [see below] and spread rapidly to European and American gardens, as can be seen by herbarium specimens and old nursery catalogues. A variety with blush flowers, called white at that time, was known in England in 1813, and was introduced to France by Louis Noisette the following year. This probably came as an independent and unrecorded introduction from Japan. Philippe F. Siebold, as a result of his first stay in Japan, from 1824 to 1830, brought or sent back other garden forms of *C. speciosa*. These were the genetic basis from which a burst of new varieties were developed, mostly by Moerloose in Belgium in the early 1850's.

During all that time, in spite of its popularity in gardens, *Chaenomeles speciosa* was relatively little known by botanists. They believed it to be, following Sims (1803), Thunberg's *Pyrus japonica* which he had seen in Japan and described in 1784. As noted earlier, Thunberg erroneously described the fruit as 5-valved and the error was not corrected for many years because isolated plants of *Chaenomeles* usually do not set fruit, due to self-incompatibility. Since it did not produce fruit, *C. speciosa* (under the name *Pyrus japonica*) was thought not to be hardy and in consequence was grown in greenhouses.

Loiseleur Deslongchamps was the first one in 1815 to provide a description for this species which he called *Cydonia lagenaria*. He had seen the fruit, at a time in its development when it is contracted in the middle and he believed that when mature the fruit would have the shape of a gourd.[11] Unfortunately, Loiseleur Deslongchamps gave as synonym of his species *Pyrus japonica* Thunberg which was really what is called now *Chaenomeles japonica* (Thunb.) Lindley ex Spach so that *Cydonia lagenaria* Loiseleur is a superfluous name.

Sweet, in 1818, realized that *Pyrus japonica* Thunberg and the plant cultivated in European gardens were different. He called the latter *Cydonia speciosa*, giving as sole character separating his new species from Thunberg's the fact that his was "cluster-flowered" versus flowers "two by two" (bini) in the first one. This distinction is of no value for Thunberg's species, in cultivation, has flowers in clusters of (1) 2 to 3 (4) and *C. speciosa* of (1) 2 to 6. Nevertheless, Sweet cites plate no. 692 (not 629, a printing error) of the Botanical Magazine, and there can be no doubt as to which plant the name "speciosa" applies. This plate, the type of the species, since no herbarium specimen was preserved, represents a flowered branch surmounted by a young shoot. The flowers show long peduncles, a normal development in warm weather; it was drawn in August as indicated in the text. The specimen represented also has abnormal, semidouble, and male flowers.

In spite of the fact that Sweet was correct, in 1818, the nomenclatural confusion was not clarified for nearly a hundred years. Nurserymen went on calling this plant *Pyrus japonica* Thunberg, *Malus japonica* (Thunb.)

[11] Loiseleur Deslongchamps says "au 4e mois de son developpement." It must have been much younger, from its shape, and also its size, given as "12 à 15 lignes de long," corresponding to 25 to 30 mm.

Andrews, *Cydonia japonica* (Thunb.) Persoon, or *Chaenomeles japonica*, names which are synonyms of the preceding species. Beside the incorrect identification made originally by Sims, some botanists seeing the plants in cultivation only, thought of them as conspecific. This is why Maximowicz (1873) proposed the name *Chaenomeles japonica* var. *α genuina* for the shrub commonly cultivated in Europe, which Ito (1900) transferred to the genus *Cydonia* as *Cydonia japonica* var. *genuina* (Maxim.) Ito. Maximowicz states that he had seen it growing with var. *pygmaea* in thickets near Yokohama. No specimen of var. *α genuina* was preserved by Maximowicz, or even annotated by him, but a herbarium sheet, kept at the British Museum, shows what are now called *Chaenomeles japonica*, and *C. speciosa*, both collected by Bisset near Yokohama, though at ten years' interval, in 1867 and 1877. It is possible that *C. speciosa* was found there as an escape from gardens.

The fact that *C. speciosa* is widely cultivated and escapes occasionally has been a source of confusion as to its real origin. There is no doubt, however, that this species is not native in Japan where it was introduced around 1550 A.D. from China (Hara, 1957). In cultivation in Japan for such a long time, *C. speciosa*, basically a variable species, has produced several garden forms, differing from the type mostly in the color of the flowers. This variability, and the undetermined center of origin of *C. speciosa*, induced Japanese botanists to name numerous "species," among them *C. angustifolia* and *C. eugenioides* Koidzumi; *C. trichogyna*, *C. cardinalis*, *C. eburnea*, and *C. extus-coccinea* Nakai. The last three names were attributed by Nakai to Carrière, a French botanist. Carrière himself (1872) did not believe them to be species and called them varieties. For *Chaenomeles eburnea* he says "c'est une espèce (?) japonaise introduite par feu Siebold." He knew the other two, 'Cardinalis' described by Lemaire in 1856, and 'Extus-Coccinea', first called 'Nivea Extus Coccinea' by Van Houtte in 1867, to have originated in European gardens. Later Carrière (1876) returned to the question of the number of species in the genus *Chaenomeles*, and recorded the variability he had already observed in the fruits, the flowers, and the inflorescences of the one species cultivated at the time in Europe. He formulated a question about Siebold who thought that every color form he saw in Japanese gardens was a different species. "Qu'aurait donc fait ce botaniste si, au Japon il eût rencontré les centaines de variétés que fournissent les semis qu'on fait de ses graines?" The names "cardinalis", "eburnea", and "extus-coccinea" can not be attributed to Carrière for he states clearly that he does not consider them to be species and as varieties they were not described first by him. In spite of the numerous combinations made by Japanese botanists for these names which are still in use in Japanese works, the "species" of Koidzumi and Nakai, mentioned above, prove to have originated in gardens and are better treated as cultivars of *Chaenomeles speciosa*.

The only uncertainty about this species concerns its center of origin

in China. The region is inaccessible now, and old herbarium labels provide very few, if any, data. A specimen which is not inscribed "cultivated" does not, as a consequence, come from a wild plant. This can be easily noticed by the numerous specimens collected in Europe, in America, or in Japan which have no indication that they were collected in gardens. Wilson, for example, does not always write "cultivated" on his labels, but Rehder (1915) states that Wilson never saw wild plants of *Chaenomeles speciosa* (as the typical form of *C. lagenaria*) in his travels in China. Rehder (1924) believes this species to be "wild on the Tsinling shan range in Shensi and eastern Kansu and cultivated elsewhere." This assumption does not seem probable. From the specimens examined, one only from Shensi, and one from Kansu are not formally indicated as cultivated, both without indication of habitat. To make things more difficult, the habitats in China, as recorded, could shelter plants escaped from cultivation; as it is known that *Chaenomeles speciosa* is commonly cultivated there for its medicinal properties. Yunnan, where the plant is also cultivated, is the province represented by more specimens without indication of cultivation, and is probably its native area. The only plant found in a forest, a wild habitat, was collected in Yunnan (*Tsai 56441*).

This probable native area of Yunnan and vicinity suggests *Chaenomeles speciosa* and *C. cathayensis* to be sympatric, but the material and data are still too scanty to be sure. Even in the same province, the two species have never been collected wild in the same localities. From data recorded on herbarium labels, *C. cathayensis*, with a wider distribution, seems to grow wild at higher elevations than *C. speciosa*. The two are closely related, but nevertheless may be distinguished easily, even in sterile condition, *C. cathayensis* growing closer to, or in the snow range, is a species larger in all its parts than *C. speciosa* of medium altitudes. This discredits the supposition that the first one is an alpine form of the other. There are no intermediates in herbaria, and specimens can be assigned to one or the other species without doubt. It is only in gardens that artificial hybrids have been produced.

The numerous forms of *Chaenomeles speciosa* can not be distinguished as varieties. They differ in the color of the flowers, the shape and size of the leaves and the fruits, the pubescence of the styles, etc. These differences appear at random in wild plants, and are not correlated with each other, or with habitat or geographical distribution. Due to this original variability, numerous cultivars have been selected from seedlings and are reproduced vegetatively. They show in a single species variation of color which is not found elsewhere in the whole subfamily of the Maloideae. The antiquity of *C. speciosa* as an ornamental must be considered. Its beauty has been appreciated in Japan for four hundred years, and in Europe and America for over one hundred and fifty. From the multitudes of seedlings which were possibly raised, less than one hundred and fifty were retained as cultivars. Beside a complete array of flower color from white to the darkest red, through pink and scarlet, the plants

show single, semidouble and double flowers, differences in the leaves and the fruits, as well as habit of varied size, with normal, pendulous or twisted stems.

3. **Chaenomeles cathayensis** (Hemsley) Schneider, Ill. Handb. Laubh. **1**: 730. *f. 405 p-p2, f. 406 e-f.* 1906, non *Pyrus cathayensis* Hemsley in Forbes & Hemsley, Jour. Linn. Soc. **23**: 257. 1887.

*Cydonia cathayensis* Hemsley in Hooker, Icon. **27**: *pl. 2657, 2658.* 1901. Lectotype, Hupeh, *Henry 5263* (K; isotype, GH); *1916* (syntype, K, not seen).
*Chaenomeles lagenaria* var. *cathayensis* (Hemsley) Rehder in Sargent, Pl. Wilson. **2**: 297. 1915.
*Cydonia japonica* var. *cathayensis* (Hemsley) Cardot, Bull. Mus. Hist. Nat. Paris **24**: 64. 1918.
*Chaenomeles speciosa* var. *cathayensis* (Hemsley) Hara, Jour. Jap. Bot. **32**: 139. 1957.
*Chaenomeles lagenaria* var. *wilsonii* Rehder in Sargent, Pl. Wilson. **2**: 298. 1915. Holotype, Western Szechwan, Mo-hsi-mien, village southeast of Tachienlu, alt. 1800 m., October 1910, *Wilson 4120* (A).
*Pyrus japonica Wilsonii* Anonymos, Jour. Roy. Hort. Soc. **41** (3): *f. 122.* 1915–16.
*Cydonia japonica* var. *wilsonii* (Rehd.) Beckett, Gard. Chron. III. **66**: 22. *f. 9–10.* 1919.
*Chaenomeles japonica* var. *wilsonii* (Rehd.) Silva Tarouca & Schneider, Uns. Freiland Laubg. 143. 1922.
*Cydonia cathayensis* var. *wilsonii* (Rehd.) Bean, New Fl. & Silva **2**: 191. 1930.
*Chaenomeles cathayensis* var. *wilsonii* (Rehd.) Bean, Roy. Hort. Soc. Dictionary of Gardening **1**: 444. 1950.
*Chaenomeles speciosa* var. *wilsonii* (Rehd.) Hara, Jour. Jap. Bot. **32**: 139. 1957.

Shrubs or small trees up to 6 m. (usually much smaller in cultivation) with sparse straight-erect branches, armed with short lateral branchlets terminated by a spur. Young shoots glabrous or pubescent; the second year ones completely glabrous. Leaves elliptic or lanceolate, 5–8 (9) cm. long and (1.5) 2–3.5 cm. broad, when young commonly covered by a thick fulvous tomentum on the under surface persisting or not at maturity, finely and sharply serrate, the serrations each terminating in an awn-like tip, rarely entire, short-petioled; stipules reniform, sharply serrate, 1–1.5 cm. long, 1–2 cm. broad. Flowers on old wood, in clusters of (1) 2–3 (6), with short pedicels. Flower buds deep rose; open flowers cup-shaped, 4 cm. broad. Sepals green to purple, depending on the amount of light. Petals white or pale pink, usually edged with rose. Stamens 40–60. Styles 5, fused at the base in a column, woolly or at least pubescent for about ½ their length; stigmata green. Pomes ovoid, green turning yellow (and red with sufficient heat), up to 15 (20) cm. long, 8 cm. broad, weighing up to 300 grams or more, skin dry. Seeds numerous, up to 120 in one fruit, usually less, 8–10 mm. long, 5 mm. broad, wedge-shaped, with two flat sides caused by compression with other seeds, the lowermost and uppermost being lenticular, brown, dull.

Blooming from March to May, depending on the latitude.

VERNACULAR NAMES. Chinese, Mu-kua; English, Chinese Quince, Quince of Cathay; French, Cognassier de Cathaye; Japanese, Ma-boke.

USES. Same as for the genus, except that due to its gaunt habit, and its lack of hardiness, it is less cultivated than the other two species of *Chaenomeles*. The fruits are used in China for making vinegar.

DISTRIBUTION. Open hillsides, thickets, river banks to evergreen forests; China, from 5000 to 7500 ft.; Tibet, from 6500 to 9500 ft.; Bhutan; Burma, from 5000 to 8000 ft.

**China.** Shansi. Chen-hai-jao. *Licent 2476* (BM, K). Hupeh. Patung Hsien, *Ho-Ch'ang Chow 1061* (A); Western Hupeh, *Wilson 2991* (A, BM, GH, US). Kwangsi. Pai-yun-an, *Tsang 27610* (A, US). Kansu. Yan-pu-ko, *Meyer 1639* (A); Hoan kia ho, *Licent 5025* (K, P). Szechwan. *Wang 20528* (AAH). Kweichow. Yan-Den-Po, Tsingschen, *Teng 90340* (A). Yunnan. *Tsai 55894* (A); *Forrest 9764* (A); N.W. Yunnan, He-shu-no, *Ching 20128* (A); Wei-si-Hsien, Yeh-Chih, *Wang 67931* (A); Tong-Tchouan, *Maire 218* (A), *Maire 361* (A); between Tengyueh and Likiangfu, *Rock 8116* (A, US); Mengtz., *Hancock 496* (K); valley behind Kin-tchong-chan, *Maire*, February-March 1912 (G); dry hills behind Kin-tchong-chan, *Maire*, March 1912 (G); valley behind Kin-tchong-chan, *Maire*, March (P).

**Tibet.** Trulung, PoTsangpo Valley, *Ludlow, Sherriff & Elliot 12271* (BM); Tongkyuk, Dzona, Pome, *Ludlow, Sherriff & Elliot 12061*, fruits only (BM); Nyam Jang Chu, *Ludlow & Sherriff 1246* (BM).

**Bhutan.** Near Bongthang, *White 159* (CAI, not seen).

**Burma.** Myitkyina, *Kermode 17127* (K); Upper Burma, *Forrest 26569* (A, K); North Burma, Kang-fang, *Kingdon Ward 304a* (NY).

CULTIVATED. China, Burma, France, Netherlands, England, United States. Also: Japan, Schneider (1906); New Zealand, Harrison (1959); Egypt, Bircher (1960); Germany, Schneider (1906).

**China.** Shantung. Tsingtan (prob. cult.), *Meyer 386* (A); Hupeh. Western Hupeh, *Woon Young Chun 3713* (A), *Wilson 410* (AAH, K, NY, P). Yunnan. Yungning, about 8400 ft., *Schneider 3477* (AAH).

**Burma.** Kang-fang, *Kingdon Ward 302* (AAH, NY).

**France.** Villa Thuret, Antibes, cult. from seeds of Wilson's 1362. *Poirault*, received April 1, 1919 (P).

**Netherlands.** Arboretum Wageningen, cult. under no. 6875, and *ibid.*, cult. under no. 3644, *Steenbergen & Prehn*, April 11, 1961 (AAH).

**England.** Royal Botanic Garden, Kew, *Nicholson*, Oct. 1881 (AAH, K), April 26, 1962 (A).

**United States.** Arnold Arb., Jamaica Plain, Mass., cult. under no. 971–25, *Rehder*, Sept. 20, 1927 (AAH), cult. under no. 146–36, *Palmer*, Aug. 5, 1941 (AAH), cult. under no. 287–61, *Weber*, Sept. 1962 (AAH). Morris Arb., Philadelphia, Pa., *Fogg*, May 17, 1960 (AAH). U.S. Nat. Arb., Washington, D.C., *Jefferson*, Aug. 1961 & Apr. 24, 1962 (AAH). Stanley M. Rowe Arb., Cincinnati, Ohio, *Weber*, May 23, 1962 (AAH); Holden Arb., Mentor, Ohio, *Lipp*, May 1961 (AAH), *Weber*, May 28, 1962 (AAH). Richland Co., Illinois, *Ridgeway 1934* (AAH).

In 1887, when Hemsley first published his *Pyrus cathayensis*, he gave as synonym *Cydonia sinensis* (Du Mont de Courset) Thouin, a good and validly published species. However, the name *Pyrus cathayensis* was not superfluous at the time, if this species was considered as belonging to the genus *Pyrus*, since there was already a *Pyrus sinensis* Lindley, which is a completely different taxon. After listing the synonyms, Hemsley noted that Henry's specimens of "Chinese Quince" and the plant cultivated at Kew "have much narrower, less hairy leaves than that originally described and cultivated in Europe." Henry's specimens and "the plant cultivated at Kew" proved to be what is now called *Chaenomeles cathayensis*.

In the fall of 1900, the director of Kew Gardens brought from the garden of Sir Thomas Hanbury, at La Mortola, Italy, fruits of the true *Cydonia sinensis*. It was immediately recognized that the plant growing at Kew under this name, synonym of *Pyrus cathayensis* Hemsley was a different and yet undescribed species. Hemsley (1901) called it *Cydonia cathayensis*, provided a Latin diagnosis and two plates showing leaves, an inflorescence, an open fruit and seeds, as well as details of the flower and the serration of the leaf. The collections Hemsley cited are Henry's specimens collected in Hupeh, the only ones the Kew Herbarium possessed from China at that time, from which a lectotype has been chosen. This first confusion of *Chaenomeles cathayensis* with *Cydonia sinensis* is still reflected in the English name "Chinese Quince," common to both species.

Just as *Chaenomeles cathayensis* was introduced and grown at Kew for more than 20 years under a different, and incorrect, name, *Cydonia sinensis*, it was later, in 1915, exhibited at the Royal Horticultural Society in London and given an Award of Merit under another incorrect name, *Cydonia mallardii*. The name 'Mallardii' properly belongs to a cultivar of *Chaenomeles speciosa*.

In 1906, Schneider transferred this species from *Cydonia* to *Chaenomeles*. He mentioned having seen specimens from Shensi (*Giraldi 5115, 5116, 5117*) and stated that the plant is so closely related to *Chaenomeles speciosa* (as *C. japonica*) as to be perhaps only a variety of it.

In 1915, Rehder transferred *Chaenomeles cathayensis* (Hemsley) Schneider to varietal rank under *C. speciosa* (as *C. lagenaria*), and described another variety, *Chaenomeles lagenaria* var. *wilsonii* differing from var. *cathayensis* by its "dense fulvous tomentum of the underside of its leaves." He noticed, however, that the young seedlings raised from seeds of the type plant, collected by Wilson (as well as from another seed collection from China, *Wilson 1362*) are "quite glabrous" and that "the constancy of this character seems doubtful." After more plants of *C. lagenaria* var. *wilsonii* had been raised from seeds, Bean (1930) expressed doubt as to the difference between the two varieties. Bean proved to be right. The character of the fulvous tomentum on the under surface of the leaves is correlated neither with geographical or ecological distribution nor with morphological characters of the wild plants. Since glabrous or

pubescent leaves when young (but on adult plants) seem to appear at random, varietal rank is not justified.

Bean also strongly criticized Rehder for placing *C. cathayensis* as a variety of *C. lagenaria* (now *C. speciosa*). He wrote, "In these days, when it is the fashion to make new species on the slightest provocation, it looks like mere perversity to unite *lagenaria* and *cathayensis*." He transferred var. *wilsonii* from *Chaenomeles lagenaria* to *Cydonia* as *Cydonia cathayensis* var. *wilsonii*. These two species, when grown side by side are very different, and can only be considered conspecific when known from inadequate herbarium specimens.

The fact that the leaves of young seedlings of pubescent forms are glabrous indicates that *Chaenomeles cathayensis* is the only species of *Chaenomeles* having markedly different juvenile leaves. These, as well as the stipules, are very narrow, always glabrous, and more sharply serrate than the leaves of adult plants, the latter sometimes being nearly entire.

Compared to the other two species of *Chaenomeles* represented in cultivation by numerous cultivars, *C. cathayensis* shows very little variation. Its two former varieties can not be maintained, and it does not have any cultivars. This is certainly due to the fact that in Europe and in America, the Quince of Cathay is rarely cultivated as an ornamental, being almost limited to botanic gardens and arboreta. Furthermore, as it is still being reproduced by seeds, nearly all the shrubs existing in cultivation can be traced to the few original seeds brought back from China by Wilson. In *C. japonica* and *C. speciosa* many seedlings were raised after their introduction to Europe, the selected ones being later reproduced by asexual means. Not enough time and attention has been given to *Chaenomeles cathayensis*. Whether or not the flower color varies, there are differences in the shape of the leaves, and of the fruits which could be selected. Local varieties probably exist in China, where the species has been in cultivation for a longer time, as well as in the wild.

If *C. cathayensis* is not used much as an ornamental, it has been tried repeatedly for its abundant production of large fruits. These are inferior in cooking qualities to the other species of *Chaenomeles* and *Cydonia*, and unpleasant to harvest because of the numerous and vicious spurs. The fruits also need more heat to ripen than any other species. Slate (1941) tested, in Geneva, N.Y., more than 350 plants of *C. cathayensis* for the commercial production of pectin or l-malic acid. His plantation was devastated by two cold winters. In contrast to other authors amazed by the fruit productivity of this species, he reports its unproductiveness. This can be explained by the self incompatibility of *Chaenomeles*. If two cultivars or species are grown side by side in a garden, the production of fruits is abundant. Isolated shrubs, or shrubs of the same kind grown together produce no fruit.

Although *Chaenomeles cathayensis* has not had much horticultural success its best qualities have been passed to interspecific hybrids which have produced numerous excellent cultivars.

4. **Chaenomeles × superba** (Frahm) Rehder, Jour. Arnold Arb. 2:58. 1920. (*Chaenomeles japonica* × *speciosa*). Lectotype, 'Superba', Arnold Arb. no. 5108 (not 5708 as written on the label), Jamaica Plain, Mass., *Rehder*, May 3, 1921 (AAH).

*Cydonia maulei* var. *superba* (Frahm) Leichtlin ex Zabel in Beisner *et al.*, Handb. Laubh.-Benenn., 182. 1903.

*Chaenomeles eugenioides* var. *superba* (Frahm) Nakai, Bot. Mag. Tokyo 37: 72. 1923.

Shrubs usually 120–150 cm. high; branches numerous, erect-spreading with slender spines. Young shoots covered with short and scabrous tomentum; the second year ones verruculose. Tomentum variable in amount, and when scantily present may indicate a backcross to *C. speciosa*. Leaves intermediate in shape, size, and serration between the parents, but usually more like *C. japonica*. Spring flowers on old wood, very abundant, in clusters of 2–6, with short pedicels; open flowers cup-shaped to flat, 3–5 cm. broad. Petals white, pink, orange or red. Styles 5, fused at the base in a column, glabrous, glabrescent or hairy. Pomes of variable shape and size, up to 6 cm. long and broad, often with a slightly viscid skin. Seeds numerous, 6–8 mm. long, 4–5 mm. broad, ovoid, pointed at one end, reddish-brown, shiny.

Blooming from March to June, depending on the latitude, but also with a few flowers during the rest of the year, weather permitting.

VERNACULAR NAME. "Superba group" in horticulture.

USES. Cultivated as an ornamental.

DISTRIBUTION. Not found wild, since the parental species have a disjunct distribution.

CULTIVATED. Japan, Poland, Germany, France, Italy, Netherlands, England, United States. Also: New Zealand, Harrison (1959); Canada.

**Japan.** Honshū. Yamanashi pref., Kasukabe Exp. Station of Med. Pl., Kasukabe-shi, *Kawatani*, Apr. 10, 1961 (AAH).

**England.** Kew Gard., *Weber*, June 7, 1960 (AAH).

CULTIVARS of *Chaenomeles* × *superba*

'Abricot', Proefst., Boskoop, Neth., *Roberts*, Apr. 5 & June 27, 1961 (AAH).

'Alba', Villa Lauterbach in Stabelwitz, Wroclaw (formerly Breslau, Germ.) Poland, *Baenitz*, May 14, 1908 (AAH); Arnold Arb. no. 5104, Jamaica Plain, Mass., *Rehder*, May 3, 1921 (AAH).

'Benichidori', Villa Taranto, Verbania-Pallanza, Italy, spring 1962 (AAH).

'Boule de Feu', Arnold Arb. no. 47–50, Jamaica Plain, Mass., *Weber*, May 17, 1961 (AAH).

'Cameo', Arnold Arb. no. 179–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).

'Charming', Arnold Arb. no. 663–50, Jamaica Plain, Mass., *Weber*, May 17, 1961 (AAH).

'Cole's Red', Arnold Arb. no. 645–61, Jamaica Plain, Mass., *Weber*, May 7, 1962 (AAH).
'Colette', Arnold Arb. no. 126–60, Weston, Mass., *Weber*, May 31, 1961 & May 12, 1962 (AAH).
'Columbia', Arnold Arb. no. 5102, Jamaica Plain, Mass., *Kobuski & Metcalf*, May 9, 1930 (AAH).
'Coquelicot', Arnold Arb. no. 123–59, Weston, Mass., *Weber*, May 9, 1962 (AAH)
'Coral Beauty', Arnold Arb. no. 664–50, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
'Corallina', Arnold Arb. no. 450–38, Jamaica Plain, Mass., *Palmer*, May 14, 1943 (AAH).
'Coral Sea', Highland Park no. 881–C, Rochester, N.Y., *Harkness*, May 15, 1961 (AAH).
'Crimson and Gold', Arnold Arb. no. 181–39, Jamaica Plain, Mass., *Weber*, May 17, 1961 (AAH).
'Crimson Beauty', Arnold Arb. no. 756–50, Jamaica Plain, Mass., *Weber*, May 11 & May 23, 1960 (AAH).
'Della Robbia', Morton Arb. no. 97–46, Lisle, Ill., *Schulenberg*, May 15, 1961 (AAH).
'Double Red', Arnold Arb. no. 124–42, Jamaica Plain, Mass., *Weber*, May 11 & May 23, 1960 (AAH).
'Double Vermilion', New York Bot. Gard., N.Y., *Weber*, Sept. 25, 1962 (AAH).
'Dwarf Coral', Proefst., Boskoop, Neth., *Roberts*, March 25 & June 27, 1961 (AAH).
'Early Apple Blossom', Arnold Arb. no. 200–42, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).
'Ecarlate', U.S. Pl. Introd. Sta., Glenn Dale, Md., *Preston*, May 10, 1962 (AAH).
'Elly Mossel', Proefst., Boskoop, Neth., *Roberts*, Apr. 5 & June 27, 1961 (AAH).
'Ernst Finken', Wayside Gard., Mentor, Ohio, *Weber*, May 28, 1962 (AAH).
'Etna', Proefst., Boskoop, Neth., *Roberts*, Apr. 5 & June 27, 1961 (AAH).
'Extus Acumineus', Kew Gard., Engl., Apr. 26, 1962 (AAH).
'Fascination', Proefst., Boskoop, Neth., *Roberts*, March 25 & June 27, 1961 (AAH).
'Fire Dance', Kew Gard. no. 316–56, Engl., *H71705/61* (AAH).
'Foliis Rubris', Arnold Arb. no. 2047–1 = 13017, Jamaica Plain, Mass., May 24, 1914 (AAH).
'Fructico Alba', Holden Arb., Mentor, Ohio, *Weber*, May 28, 1962 (AAH).
'Fruitlandi', Arnold Arb. no. 118–62, Jamaica Plain, Mass., *Weber*, Sept. 25, 1962 (AAH).
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When *Chaenomeles* × *superba* was described by Frahm in 1898, it was as *Cydonia maulei* (now *Chaenomeles japonica*) var. *superba*. Its hybrid nature had been suspected by Zabel (in Beisner *et al.*, 1903) but was recognized much later by Rehder in 1920. This "variety" of Frahm is now the cultivar 'Superba' regarded as the type of this complex, though other members of the Superba group originated several years earlier. By the time Rehder (1920) [12] reported his conviction that 'Superba' was a hybrid between what are now called *C. japonica* and *C. speciosa*, other "cultivars" having the same parental species had appeared spontaneously in English, German, Swiss, and French nurseries. In fact, these natural hybrids started to appear as soon as *C. japonica* (as *Cydonia maulei*) began to spread in gardens and to be grown side by side with the then common species, *C. speciosa*. One can only wonder why hybrids did not occur earlier in Japan, but the explanation could be as Makino noted (1908), *C. japonica* had not been cultivated in Japan at that time.

All or most of these forms which originated in gardens were, until Rehder's work was published (1928), believed to be varieties of *Chaenomeles japonica* (as *Cydonia maulei*) which they resemble more than the other parent. An adult shrub with full size leaves is really intermediate between the two species, but young plants, seen only in flowering condition may be easily confused with *C. japonica*, from the warting of the second year shoots and the crenate leaves. Plants more similar to *C. speciosa* are usually backcrosses to this parent.

The hybrid nature of this group of cultivars is no longer questioned. The first cross of which a record is available, was made in the Barbier Nursery, Orléans, France, before 1913, but botanists of the period were unaware of it. *Chaenomeles speciosa* 'Baltzii' and *C. japonica* 'Maulei' were used as parents. From the group of seedlings which resulted, the cultivars 'Boule de Feu', 'Ecarlate', and 'Vermilion' were selected. Many more crosses have been made since, and the hybrids have, in the field, a common bushy appearance. The hardiness, and moderate size of the

[12] *C.* × *superba* (Frahm) Rehder was validly published in 1920 without a Latin diagnosis, and without the indication of a type specimen which became mandatory only in 1935 and 1958 respectively.

shrubs make them perfectly suitable for small gardens. The flowers are usually large and abundant, and their range of color extends to the one found in the two parental species. These horticultural qualities explain why new cultivars of the Superba group are being introduced almost every year.

5. **Chaenomeles × clarkiana** Weber, 1963. Arnoldia **23**: 53. 1963. (*Chaenomeles cathayensis × japonica*). Holotype, 'Minerva', Kew Gardens no. 239–59, Engl., *H1705/61* (AAH).

Shrub of low growth, maximum size unknown. Branches erect-spreading, with spines more numerous and longer than in *C. japonica*, more slender than in *C. cathayensis*. Young shoots pubescent, the second year ones slightly verruculose. Leaves and serration intermediate between the two parents in shape and size (small and narrow in 'Cynthia', large and broad in 'Minerva'). Flowers large, 4–5 cm. broad, pink to rosy-red. Pomes medium sized, maximum 6 cm. long by 6 cm. broad, apple- to orange-shaped, skin dry or slightly viscid. Seed numerous, 8 mm. long, 4–5 mm. broad, ovoid, pointed at one end, with two flat sides from compression, brown, dull or slightly shiny.

VERNACULAR NAMES. Miniature Cathayensis hybrids, Clarkiana group (of horticulture).

USES. Rarely cultivated as an ornamental.

DISTRIBUTION. Not found wild, since the parental species have a disjunct distribution.

CULTIVATED. England, United States.

CULTIVARS of *Chaenomeles × clarkiana*

'Cynthia', Du Pont Gard., Winterthur, Del., *Tyrell*, Apr. 1961 (AAH).
'Minerva', Morton Arb. no. 58–58, Lisle, Ill., *Schulenberg*, spring 1962 (AAH).

This hybrid group is named for the late Walter B. Clarke, nurseryman of San Jose, California, who first produced the hybrids. He crossed *C. cathayensis* and *C. japonica* to produce a shrub having the large flowers of the first parent, and smaller size from the influence of *C. japonica*. In 1945, Clarke selected from the complex two cultivars calling them "Miniature Cathayensis hybrids." So far, they have not had much success in gardens, due mainly to their lack of hardiness, and the fact that they did not add any new shade of color to the well known cultivars of the Californica group.

6. **Chaenomeles × vilmoriniana** Weber, 1963. Arnoldia **23**: 64, 65. 1963. (*C. cathayensis × speciosa*). Holotype, 'Afterglow', U.S. Nat. Arb., Washington, D.C., *Jefferson*, Apr. 24, 1962 (AAH).

Shrubs about 2–2.5 m. high, with stiff branches, erect as in *C. cathayensis*, but more numerous, armed with spurs or strong spines. Young shoots glabrous or sparsely pubescent; second year shoots completely smooth. Leaves elliptic to ovate (when young with a light fulvous tomentum on the under surface), sharply serrate, with the serration usually terminating in an awn-like tip. Flowers large, white, suffused with pink, as in *C. cathayensis*. Pomes few, ovoid, approximately 8 cm. long, 5–6 cm. broad, skin dry. Seeds numerous, usually 10 mm. long, 4–5 mm. broad, wedge-shaped, with two flat sides from compression, brown, dull.

VERNACULAR NAMES. Vilmoriniana group of horticulture.

USES. Cultivated as an ornamental.

DISTRIBUTION. Not observed in the wild, although the two parental species are sympatric.

CULTIVATED. France, Netherlands, England, United States.

CULTIVARS of *Chaenomeles* × *vilmoriniana*

'Afterglow', Mount Airy Arb., Cincinnati, Ohio, *Weber*, May 22, 1962 (AAH).
'Mount Everest', Arnold Arb. no. 513–55, Jamaica Plain, Mass., *Weber*, May 16 & May 23, 1960 (AAH).
'Vedrariensis', Kew Gard. no. 910.31, Engl., *Weber*, June 7, 1960 (AAH).

This hybrid group is named for the late Philippe de Vilmorin, Verrières-le-Buisson, France, who, in the spring of 1921, made the cross from which the first cultivar of this group was raised. He used pollen of *Chaenomeles speciosa* (as *C. japonica*) to pollinate flowers of *C. cathayensis*. More than one hundred seeds were collected and sown in December of the same year. The hybrid was sold to Victor Lemoine, nurseryman at Nancy, France, who introduced it in 1928, under the name of *Chaenomeles hybrida*, later *C. hybrida vedrariensis*. It was never described, even in a nursery catalogue, but the name "vedrariensis" was nevertheless picked up in *Index Kewensis*, Supplements 9 and 12, following a presentation of the fruits [13] to the Société Dendrologique de France on October 18, 1934. *Chaenomeles vedrariensis* Hort. is a nomen nudum and the plant is better treated as 'Vedrariensis', a cultivar belonging to the Vilmoriniana group.

Before World War II Clarke, in San Jose, California, gathered a living collection of *Chaenomeles* including the three species and all varieties then available, in order to breed improved ones for modern gardens. In 1940, he introduced 'Mount Everest' which appeared in his nursery as a chance seedling, and which he thought was a hybrid between *C. cathayensis*

[13] In the notes left by A. Meunissier, former director of the *Service Experimental* at the firm de Vilmorin, it was said that the original plant (as a proof of its hybrid nature), possessed usually aborted female organs. This is frequent in the entire genus *Chaenomeles*, although some fruits with good seeds can be found.

(considered a good species by him, in spite of Rehder's opinion) and *C. speciosa* (as *C. lagenaria*). This supposition [14] made by Clarke when he registered the cultivar through the American Association of Nurserymen, seems to be correct. The botanical characters of 'Mount Everest' are intermediate between the two species, while 'Vedrariensis' is more closely related to *C. cathayensis*. The last cultivar of this group 'Afterglow' is, according to Clarke, "a seedling of 'Mount Everest' which it resembles in most ways except that it has double flowers."

This hybrid group, at least as far as the last two cultivars are concerned, is a real improvement on most other white-flowered varieties. The shrubs with their long serrate leaves are vigorous and handsome, but their lack of hardiness limits their use in areas with cold winters.

7. **Chaenomeles × californica** Clarke [15] ex Weber, 1963. Arnoldia 63: 50–53. 1963. (*Chaenomeles cathayensis* × *superba*). Lectotype, 'Rosemary', Univ. of Washington Arb. no. 2180–41, Seattle, Wash., *Witt*, Apr. 22, 1961 (AAH).

Shrubs usually 1.8–2 m. high. Branches stiff, erect as in *C. cathayensis*, but more numerous, strongly armed with spurs. Young shoots sparsely pubescent; those of the second year with a few warts. Leaves lanceolate, sometimes with a light fulvous tomentum on the under surface when young, serration intermediate between the parents. Flowers large, 4–6 cm. broad, usually pink or rosy-red, or often a blend of the two. Pomes 6 (8) cm. long, 6 cm. broad, ovoid, apple- or orange-shaped, skin dry or slightly viscid. Seeds numerous, usually 9 mm. long, 5 mm. broad, ovoid, pointed at one end, brown, dull or slightly shiny.

VERNACULAR NAMES. Cathayensis hybrids, Californica group of horticulture.

USES. Cultivated as an ornamental.

DISTRIBUTION. An artificial hybrid.

CULTIVATED. New Zealand, Germany, France, Netherlands, England, United States.

CULTIVARS of *Chaenomeles × californica*

'Arthur Colby', Morton Arb., Lisle, Ill., *Weber*, May 24, 1962 (AAH).
'California', Arnold Arb. no. 176–39, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).

[14] Clarke at first put all the hybrids of *C. cathayensis* in his new group Californica.
[15] The name "californica" proposed for this hybrid group by Clarke, in 1940, was without Latin description, and hence invalid. Since it has been widely used in horticulture, I have retained the name and validated it by supplying a Latin description.

'Cardinal', Michigan State Univ., East Lansing, Mich., *Parmelee*, spring 1962 (AAH).

'Clarke's Giant Red', Arnold Arb. no. 751–60, Weston, Mass., *Weber*, May 31, 1961 (AAH).

'Enchantress', Arnold Arb. no. 178–39, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Fire', Arnold Arb. no. 511–55, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Flamingo', Michigan State Univ., East Lansing, Mich., *Parmelee*, spring 1962 (AAH).

'Masterpiece', Arnold Arb. no. 180–39, Jamaica Plain, Mass., *Weber*, May 6, 1960 (AAH).

'Pink Beauty', Arnold Arb. no. 340–41, Jamaica Plain, Mass., *Weber*, May 6 & May 23, 1960 (AAH).

'Rosemary', Orland E. White Arb., Boyce, Va., *Wagenknecht* 5309 (AAH).

'Rosy Morn', Arnold Arb. no. 181–58, Weston, Mass., *Weber*, May 31, 1961 (AAH).

'Sunset Glow' ('Sunset Gold'), Univ. of Washington Arb. no. 2185–41, Seattle, Wash., *Witt*, Apr. 22, 1961 (AAH).

This hybrid group which is a synthesis of the three species of *Chaenomeles* is the result of a cross made by Clarke, using *C. cathayensis* and *C.* × *superba* 'Corallina' as parents. In 1938, Clarke selected several cultivars, offered them under numbers for sale the following year, with the collective name, *Chaenomeles cathayensis* hybrids. In 1940, four [16] were named, 'Enchantress', 'Masterpiece', 'Rosemary', and 'Sunset Glow', and the group which Clarke considered to "constitute a new and entirely distinct species" was called by him *Chaenomeles californica*. He gave a horticultural description in English. Later on, criticized by botanists, he abandoned this name, and to complicate matters, named 'California' a cultivar belonging to the same group. This name, *C.* × *californica*, however, is widely used in horticulture. In order to validate it, in accordance with the *International Code of Nomenclature for Cultivated Plants*, a Latin diagnosis was provided in my earlier paper (Weber, 1963).

In the fifteen years after making his original cross, Clarke introduced many cultivars, named or under numbers, selected from the first seedlings, or from the second or even the third generation. No one, so far, seems to have duplicated the cross *C. cathayensis* × *superba*, but there are still cultivars being selected which have this formula from one of their parents.

The cultivars of the Californica group have had a wide and well deserved acceptance, because of the abundance, size, and bright colors of the flowers. Unfortunately, the shrubs lack hardiness, like *C. cathayensis* one of the parental species. Also, like *C. cathayensis*, they have a tendency to be "stiff." The only polyploid found so far in *Chaenomeles* is 'Clarke's Giant Red'; its straggly habit, however, detracts from its beautiful large flowers.

[16] In reality five, 'Mount Everest', a chance seedling, being also in this list. It is a member of the Vilmoriniana group.

SPECIES EXCLUDENDA

*Chaenomeles chinensis* (Du Mont de Courset) Koehne, Gartenflora 61. 1891 = *Cydonia sinensis* (Du Mont de Courset) Thouin.

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Numerous articles are available on the pomology of apples and pears, and their conclusions may be applied also to Japanese Quinces. A selection of these references has been supplied. The nursery catalogues which are often the places of publication of the names of cultivars are not cited in this bibliography but may be found in the publication *Cultivars in the Genus Chaenomeles*, which is, in part, a registration list of the cultivars (Arnoldia 23: 17–75. 1963).

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# THE GENERA OF CISTACEAE IN THE SOUTHEASTERN UNITED STATES [1]

GEORGE K. BRIZICKY

CISTACEAE Jussieu, Gen. Pl. 294. 1789, "Cisti," nom. cons.

(ROCKROSE FAMILY)

Shrubs, subshrubs, or herbs, often pubescent. Leaves alternate [or typically opposite], simple, entire, pinnately [or palmately] nerved, or sometimes 1-nerved, usually relatively small and narrow, usually bifacial, stipules present or absent. Flowers bisexual, regular, hypogynous, solitary or in cymose (pleio- or monochasial) terminal or axillary inflorescences. Sepals 5 (the outer 2 often bractlike, conspicuously narrower than the inner) or 3, distinct, convolute in bud. Petals 5, rarely 3, or absent (cleistogamous flowers), convolute (in the opposite direction to that of the sepals) in bud, rarely imbricate, usually ephemeral, very rarely persistent. Stamens numerous, rarely 3–10; filaments distinct, sometimes sensitive; anthers basifixed, 2-locular at anthesis, longitudinally dehiscent; pollen usually 3-colpate, suboblate to prolate, medium sized to large, of various patterns, often reticulate. Gynoecium of 3 [5–10] united carpels; style simple, long to very short or wanting; stigma 1, either large and capitate or discoid (often 3[5–10]-lobed) or minute, or stigmas rarely 3, fimbriate-plumose; ovary 1- or imperfectly 3[5–10]-locular, placentae parietal, filiform or shieldlike, often intruded; ovules 2 to many on each placenta, funiculate, orthotropous [rarely anatropous], with 2 integuments and a thick nucellus. Capsule loculicidal, 3[5–10]-valved, 3- to many-seeded. Seeds usually small, with starchy, often hard endosperm (nuclear in development); embryo curved in the form of a hook or ring, or ± circinate [or plicate to biplicate], rarely almost straight; seed coat of 2 integuments,

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296–346. 1958) and continued through those in volumes 40–45 (1959–1964). The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

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the outer thin, delicate, membranaceous, often gelatinous when moist, sometimes collapsed and deformed, the inner hard. TYPE GENUS: *Cistus* L.

A family of seven genera and about 200 species, primarily of the warm-temperate regions of western Eurasia, North Africa, North America, and South America (a few species of *Helianthemum* subg. *Lecheoides* in Chile, southern Brazil, Uruguay, and Argentina), with the strongest concentration of species in the Mediterranean region, especially the Iberian Peninsula. There are notable extensions northward into the subarctic (*Helianthemum nummularium*, in Karelia in Europe; *Hudsonia tomentosa* Nutt., in northern Alberta and probably in southern Mackenzie in North America) and southward into the tropics (a few *Helianthemum* species in the western Sahara, one in the mountains of central Costa Rica, and two in Hispaniola). In North America the family is represented by *Hudsonia*, *Lechea*, and subg. *Lecheoides* of *Helianthemum* and is centered in the Atlantic Coastal Plain.

Cistaceae, in general, are chamaephytes inhabiting dry, sunny sites in lowlands to mountains (rarely at high altitudes) and often showing a preference for sandy soils. Reproduction by fragmentation of underground stolons has been recorded in some Old World species of *Cistus* and *Helianthemum* (Gaume).

An ecto- and endotrophic mycorrhizal association has been found in *Helianthemum nummularium* (Boursnell). The fungus, which spreads through the plant and infects the outer "gelatinous" coat of the seeds, is necessary for germination, apparently supplying the developing seedling with thiamin, without which the young plant will not grow. A fungus in the seed coat and roots is probably found throughout the Cistaceae, as is suggested indirectly by the absence of root hairs in all seedlings of 15 species of *Helianthemum*, *Cistus*, *Tuberaria*, and *Fumana* which Gaume investigated.

Apparently there are no adaptations for seed dispersal, although it has been suggested that the gelatinization of the outer seed coat in moist weather could favor dispersal by small animals. Usually the seeds falling from the capsules seem to remain close to the parent plant. Germination is epigeal. Starch grains have been found in the epidermis of the outer seed coat in several genera.

Glandular (uniseriate and sometimes capitate) and nonglandular (simple, "falsely bicellular," tufted, stellate and rarely peltate) hairs are useful in at least some cases in distinguishing the species. The simple, "falsely bicellular" hairs, which appear (when mature) to have a second hair included in their basal portion, have been recorded only in Cistaceae (*Lechea*, to some extent in *Hudsonia*, and sporadically in other genera) and in Combretaceae.

The flowers usually open in sunshine, sometimes for only a few hours. They are visited for pollen by a variety of hymenopterous, dipterous, and coleopterous insects. Complete self-sterility has been observed in *Cistus*, and some European species of *Helianthemum* seem to be more or less self-

incompatible. In most other genera cross-pollination and self-pollination have been reported, the latter occurring in the case of failure of insect pollination. Cleistogamy is widely distributed, occurring either occasionally in normally chasmogamous species (e.g., some species of *Cistus*, *Tuberaria*, and the European and American subgenera of *Helianthemum*) or, as a rule, in several species of *Fumana* and *Helianthemum* sect. *Eriocarpum* and in most of the species of sect. *Lecheoides*. Polyembryony has been recorded in *Cistus hirsutus* Lam. and *Helianthemum grandiflorum* Kerner.

Numerous natural and artificial interspecific hybrids in *Cistus*, *Halimium*, and *Helianthemum* sect. *Helianthemum* are known, and hybrids in *Lechea* seem probable. A hybrid origin for *Hudsonia tomentosa* var. *intermedia* Peck has been suggested (Hall). About 15 more or less fertile natural intergeneric hybrids (× *Halimiocistus*) between species of *Cistus* sects. *Halimioides* and *Halimium* are known. Chromosome counts, including only one on an American species, cover about 20% of the family and a very limited part of the ranges of the species. The family appears to be aneuploid (*Cistus*, $2n = 18$; *Halimium*, $2n = 18$; *Helianthemum*, $2n = (10), 20, 22$; *Tuberaria*, $2n = 14, 24, 36, 48$; *Fumana*, $2n = 32$). All the counts in *Cistus*, the most primitive genus, suggest nine as the basic chromosome number of the family. On this basis, polyploidy (at present evident only in *Tuberaria* and *Fumana*) seems to be rare but probably played a part in the origin of some species and genera. Chromosome numbers, as well as pollen morphology (Heydacker), appear to support the existing classification of the genera and sometimes of subgenera of Cistaceae.

Cistaceae are most closely related to Bixaceae, but a relationship with Violaceae through Flacourtiaceae seems very probable. An affinity to Capparales, especially Resedaceae and Capparaceae, has also been suggested. A close relationship between Cistaceae and Hypericaceae has been disproved and the considerable similarities of these families explained by parallel evolution (cf. Vestal).

Economically the family is of slight significance. Two Mediterranean species of *Cistus* yield ladanum or labdanum, a fragrant oleoresin used in incense and perfumery. The young shoots of *Helianthemum canadense* contain about 10% tannic acid and a *Helianthemum*-glucoside. The species is said to be used as a remedy against scrofulae, and the local use of shoots of *Lechea villosa* (*L. mucronata*) as a tonic and febrifuge has been recorded. Several species of *Cistus*, *Halimium*, and *Helianthemum* are grown as ornamentals.

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## KEY TO THE GENERA OF CISTACEAE

A. Petals 5, convolute in bud, yellow, fugacious, or wanting; stigma 1; ovary and capsule 1-locular with filiform placentae.
  B. Leaves with flat or merely revolute blade, flowers (our spp.) of two kinds, the earlier chasmogamous with broad petals, the later cleistogamous with petals reduced or more often wanting; style short or wanting, stigma large, usually capitate, often ± 3-lobed; embryo curved in the form of a hook or ring to ± circinate; erect subshrubs or perennial herbs. ..... 1. *Helianthemum.*
  B. Leaves scalelike or subulate; flowers uniform, with relatively narrow petals; style elongate, slender, stigma minute; embryo coiled into the form of a closed hook; bushy, heathlike, low subshrubs. .. 2. *Hudsonia.*
A. Petals 3, imbricate in bud, reddish, marcescent; stigmas 3, fimbriate-plumose, red, sessile or subsessile; ovary and capsule incompletely 3-locular with broad, shieldlike placentae; embryo nearly straight to curved; low suffruticose or herbaceous flaxlike perennials, mostly with overwintering basal leafy shoots. ..... 3. *Lechea.*

### 1. Helianthemum Miller, Gard. Dict. Abr. ed. 4. 1754.

Herbs or subshrubs [or shrubs], usually pubescent with stellate hairs; leaves alternate [or opposite], flat, sometimes slightly revolute, pinnately veined, relatively small and narrow, 1–3.5(–5) cm. long, linear, oblong to oblanceolate, rarely obovate, usually short-petioled or subsessile, exstipulate [or stipulate]. Flowers dimorphic [or homomorphic], the earlier chasmogamous, petaliferous, often showy, the later cleistogamous, usually apetalous, sometimes cryptopetalous, pediceled to subsessile, solitary or in few- to many-flowered cymose, raceme-, corymb-, or headlike, sometimes paniculate inflorescences. Sepals 5, the 2 outer bractlike, considerably narrower, shorter to longer than the 3 inner. Petals 5, usually yellow, delicate, fugacious, longer than the sepals, or very small or wanting (in cleistogamous flowers). Stamens numerous, 12–35[–100], with long filaments, or (in cleistogamous flowers) 3–10, with short filaments. Gynoecium 3-carpellate; stigma large, usually capitate, sometimes deeply 3-lobed; style single, terminal, short [long] or wanting; ovary 1-locular, with 3 parietal filiform placentae and numerous (usually 20–80) or, in cleistogamous flowers, relatively few (mostly 3–20) orthotropous ovules on long, filiform funiculi. Capsule 3-valved, few to many seeded, seeds small, smooth, papillose, or reticulate, embryo curved in the form of a hook or ring to ± circinate [or plicate to biplicate]. (Including *Halimium* (Dunal) Willk. §§ *Spartioides* Grosser and *Lecheoides* Dunal and *Crocanthemum* Spach sensu Britton, Janchen et auct.) LECTOTYPE SPECIES: *Cistus nummularius* L. = *H. nummularium* (L.) Mill. (*H. Chamaecistus*

Mill.); see Rehder, Bibliogr. Cult. Trees Shrubs 471. 1949. Name from Greek, *helios*, sun, and *anthemon*, flower.) — SUNROSE, FROSTWEED.[2]

A genus of about 110 species in three subgenera, the range nearly that of the family. Subgenera HELIANTHEMUM (subg. *Ortholobum* Willk.) and PLECTOLOBUM Willk., with about 80 species, are restricted to the Old World. Subgenus LECHEOIDES (Dunal) Reichenb. (LECTOTYPE SPECIES: *H. corymbosum* Michx.) is exclusively American, with about 30 species in two sections: sect. LECHEOIDES, plants usually with dimorphic flowers, occurring in eastern North America and South America with extensions to the West Indies and to Mexico, Central America, and Chile (*H. hirsutissimum* Presl) and sect. SPARTIOIDES (Grosser) Brizicky,[3] broomlike subshrubs with homomorphic flowers, known from western North America (California and Mexico), and Chile (*H. spartioides* Presl). About nine species occur in our area. *Helianthemum Nashii* Britton and *H. thyrsoideum* Barnh. are restricted to peninsular Florida, while *H. arenicola* Chapm. inhabits coastal sand dunes from northwestern Florida and Mississippi. *Helianthemum carolinianum* (Walt.) Michx., *H. georgianum* Chapm., *H. rosmarinifolium* Pursh, and *H. corymbosum* Michx. are typical Coastal Plain species ranging from Florida northward to North Carolina and westward to eastern Texas and Arkansas, or northward to Virginia and westward to Mississippi (*H. corymbosum*). The two northernmost species, *H. canadense* (L.) Michx., $2n = 20$, and *H. Bicknellii* Fern., centered in the northeastern United States, but the latter reaching 53° latitude in Manitoba, extend southward to South Carolina, northernmost Georgia, and Tennessee, and the latter apparently occurs also in Arkansas.

The American species of *Helianthemum*, which differ from the Old World ones mainly in the alternate leaves, short or wanting styles, and a ring- or hooklike, curved to ± circinate (*vs.* plicate or biplicate) embryo, have been segregated by some taxonomists from *Helianthemum* (as well as from *Halimium*) as *Crocanthemum* Spach (Britton, Janchen, *et al.*) or *Heteromeris* Spach (Ponzo). The difference in the phyllotaxy is hardly essential, for in the American species the lowermost leaves sometimes are opposite and in the Old World species the uppermost alternate. Although in most species of the Old World subgenera the styles are elongated, rather

[2] The common name sunrose is applicable to the species of *Helianthemum* in general. Frostweed, now employed for designation of all the Atlantic American species of the genus, was originally applied to *H. canadense* because in this species the production of acicular ice crystals from the dead and cracked bark at the root in late autumn was first noticed. Frostwort, adopted in *Standardized Plant Names* (ed. 2, 1942, p. 144) as a common name for all the species of *Crocanthemum* (*Helianthemum* subg. *Lecheoides*) has apparently not met with general recognition. The name rushrose has been adopted for the Pacific American species. Rockrose, although often referred to the species of *Helianthemum*, was applied originally and primarily to the genus *Cistus*.

[3] **Helianthemum** subg. **Lecheoides** sect. **Spartioides** (Grosser), comb. nov. *Halimium* sect. *Spartioides* Grosser, Pflanzenreich IV. **193**(Heft 14): 33. 1903; *Crocanthemum* sect. *Spartioides* (Grosser) Janchen, Nat. Pflanzenfam. ed. 2. **21**: 305. 1925. LECTOTYPE SPECIES: *H. spartioides* Presl.

than short or wanting as in ours, the generic significance of this character seems questionable. Likewise, the distinction in the shape of the embryo does not appear to be absolute. Lubbock (pp. 188, 189) says of some European species, "The embryo of *Helianthemum*, according to Bentham and Hooker, is uncinate, biplicate, or circumflexed. Those coming under my notice are spirally coiled much in the same way as in *Cistus* . . ." Therefore, following Fernald (1917, 1941), the American species are treated here as belonging to a subgenus under *Helianthemum*. The single chromosome count reported for this subgenus, $2n = 20$, a number common in the Old World subgenera, seems to support this view. Palynological evidence also seems to favor the concept of the genus adopted here. Heydacker, who investigated pollen in 55 species in seven genera of Cistaceae (the number of species in each genus unfortunately not given) came to the conclusion that on the basis of pollen characters it would be preferable to retain certain American species, e.g., *H. canadense*, *H. corymbosum*, and *H. scoparium* Nutt. in *Helianthemum*, but in a special section ("tribu"). This conclusion apparently is extendable (on the basis of their close relationships) to all American species of *Helianthemum*, except *H. carolinianum* and *H. brasiliense* (Lam.) Pers., the well-individualized pollen of which supports (according to Heydacker) the retention of the genus *Crocanthemum* (apparently in its original delimitation as to include only these two species). However, since at present no other data which might justify the segregation of *H. carolinianum* and *H. brasiliense* are known, both are retained in *Helianthemum* subg. LECHEOIDES.

The dimorphism of the flowers is a distinguishing feature of members of sect. LECHEOIDES. The cleistogamous flowers, usually smaller than the chasmogamous, are apetalous or rarely with much-reduced petals and have a lower number of stamens and ovules. They appear either almost contemporaneously and in the same cluster with the chasmogamous or only in autumn and arranged in various inflorescences (the petaliferous then vernal and mostly solitary). No hybrids have been recorded in the subgenus.

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## 2. Hudsonia Linnaeus, Mant. Pl. 11. 1767.

Low, heathlike subshrubs with tufted, diffusely branched stems. Leaves alternate, sessile, small, isolateral, linear-subulate and ascending to spreading or scalelike and appressed and imbricated, softly pubescent, exstipulate. Flowers small, but showy, pediceled or subsessile, solitary at the end of short, leafy branchlets. Sepals usually 3, not quite alike, 1 entire, the 2 others unequally bifurcate at apex or with a tooth or a linear-subulate lobe on the margin. Petals 5, yellow, rarely whitish, obovate-oblong, considerably longer than the sepals. Stamens (8)10–30, filaments filiform, anthers small, ovate or oval in outline. Style elongate, slender, with a minute stigma; ovary 1-locular with 3 nervelike placentae, each bearing 2 orthotropous funiculate ovules. Capsule ovoid or ellipsoidal, few seeded, 3-valved, included in the persistent calyx. Seeds ellipsoidal, minutely warty on the surface; embryo coiled into the form of a closed hook. LECTOTYPE SPECIES: *H. ericoides* L.; see Britton & Brown, Illus. Fl. No. U. S. ed. 2. 2: 541. 1913. (Named in honor of William Hudson, 1730–1793,

apothecary and botanist, author of *Flora Anglica*, 1762.) — BEACH HEATHER, FALSE HEATHER.

A North American genus of three species ranging along the Atlantic coast from North Carolina to southern Labrador and Newfoundland, inland across Quebec to northern Alberta and probably southern Mackenzie, south- and eastward to North Dakota, Minnesota, Wisconsin, northern Indiana, northern Illinois, Michigan, and northeastern New York. The northernmost, the temperate-subarctic *H. tomentosa*, woolly beach heather, growing on sand dunes along the coast, shores of rivers and lakes, and on sand hills and sandy prairies and pinelands throughout most of the range of the genus, is known in our area only from the seacoast of North Carolina. The occurrence in our area of the northeastern *H. ericoides* L., golden heather, a species primarily of sandy acid pinelands and acidic rocks, seems questionable, and reports from North Carolina need verification. *Hudsonia montana* Nutt., closely related to and perhaps not specifically distinct from *H. ericoides*, is known only from the stony summit of Table Rock (and adjacent peaks in the Blue Ridge, according to Small), in Burke County, North Carolina.

Hybrids between *Hudsonia tomentosa* var. *tomentosa* and *H. ericoides* where these ecologically different species occur together (e.g., along open, sandy highway shoulders running between coastal dunes and pinelands) have been reported by Hall, who considered *H. tomentosa* var. *intermedia* Peck (*H.* × *intermedia* (Peck) Erskine) to be a putative hybrid between the two, since it shows recombinations of characters from both. "The origin of var. *intermedia* is probably not a recent development, i.e., since man built his coastal highways; but more likely in post-Pleistocene, as a result of glacial disturbances of the landscape, opportunity probably existed for these species to hybridize and for the new ecotype to become established."

The genus is quite distinctive in its bushy, heathlike habit, small isolateral leaves, prevailingly simple, woolly hairs, and three sepals. The basic number of sepals is five, but each of the two outer is completely or partially fused along its margin with the adjacent inner sepal, being apparent as a tooth or a linear-subulate lobe of the latter. Very rarely at least one of the outer sepals is almost distinct. A similar origin for the three sepals of some species of *Halimium* and *Cistus* has been reported by Saunders.

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3. **Lechea** Kalm ex Linnaeus, Sp. Pl. 1: 90. 1753; Gen. Pl. ed. 5. 40. 1754.

Subshrubs or perennial herbs [frequently biennial in the northern part of the range], subprocumbent to erect, usually strongly branched, mostly with overwintering basal leafy shoots. Leaves generally alternate (the lower cauline and those of the basal shoots sometimes subopposite, opposite, or verticillate), small, ovate to linear or subulate, bifacial, 1-nerved, exstipulate. Flowers minute, 2–2.5[–4] mm. broad, pyriform to subglobose, short-pediceled to subsessile, numerous, in leafy panicles or in raceme-like inflorescences. Sepals 5, the 2 outer linear-lanceolate to subulate, shorter to longer than the 3 ovate to obovate inner sepals. Petals 3, dark red or reddish, mostly shorter than the sepals, flat and imbricated in bud, marcescent, rarely seen expanded. Stamens 3–25, usually 5–15, filaments filiform, anthers minute, broadly ovate. Stigmas 3, fimbriate-plumose, dark red, sessile or subsessile, ovary short-stipitate, incompletely 3-locular, with 3 shieldlike placentae on incomplete partitions, each placenta usually bearing 2 erect, subsessile ovules, 1 on each side of its posterior face. Capsule narrowly ovoid or obovoid to depressed-globose, incompletely 3-locular or 1-locular, 3-valved, 1–6-seeded. Seeds small, of different shapes, usually 2- or 3-sided, equi- or inequilateral, shining or dull, smooth or reticulate; endosperm hard, sometimes almost transparent; embryo slender, nearly straight to considerably curved. LECTOTYPE SPECIES: *L. minor* L.; see Britton, Bull. Torrey Bot. Club 21: 244. 1894. (Named for Johan Leche, 1704–1764, Swedish botanist and professor of medicine in Åbo.) — PINWEED.

A genus of 17 species centered in eastern North America but extending northwestward to Saskatchewan (*Lechea intermedia* Leggett var. *depauperata* Hodgd.) and southward to Cuba (*L. cubensis* Leggett) and Guatemala (*L. tripetala* (Moç. & Sessé ex Dunal) Britton). Ten species occur in the southeastern United States: *L. cernua* Small, *L. Deckertii* Small (*L. myriophylla* Small), *L. divaricata* Shuttlew. ex Britton, *L. Leggettii* Britt. & Hollick var. *ramosissima* Hodgd., *L. minor*, *L. patula* Leggett (*L. exasperata* Small, *L. prismatica* Small), *L. racemulosa* Michx., *L. tenuifolia* Michx., *L. Torreyi* Leggett ex Britton, and *L. villosa* Ell. (*L. mucronata* Raf.). *Lechea maritima* Leggett, although reported by Small (Man. SE. Fl. 883. 1933) from our area, apparently does not occur south of Virginia.

Although the species are well defined, the specific distinctions are based on rather small technical characters. The basal overwintering shoots (lacking in *Lechea Deckertii*) which appear late in the season and bear crowded, sometimes opposite leaves (usually broader and shorter than the cauline), the calyces (especially the comparative length of the outer and inner sepals), and the fruits and seeds offer the most reliable taxonomic characters.

The species are, in general, inhabitants of dry, sandy, or gravelly,

more rarely rocky, soils near the coast and/or inland on riverbanks, in open woods, fields, barrens, open roadsides, etc. The ecology has not been studied in detail. Distributional patterns are varied. Thus, *L. villosa*, the most widely distributed species, occurs throughout most of eastern North America, south to Florida, west to Texas and northeastern Mexico, Oklahoma, and Nebraska; *L. cernua*, *L. divaricata*, and *L. Deckertii* are endemic to Florida (the last also in southern Georgia); *L. patula* is restricted to the southeastern Coastal Plain; and *L. Leggettii* var. *ramosissima* and *L. Torreyi*, both of the southeastern Coastal Plain, have noteworthy disjunctions in central Tennessee and in British Honduras, respectively.

The flowers, which appear in mid- or late summer, are reported as rarely expanded, except in early morning in bright sunshine. No reliable data are available regarding pollination and fertilization. Kearney stated that *Lechea maritima* may be "safely referred to" as a self-fertilized species, but Hodgdon thought that it "must certainly be to a considerable extent cross-fertilized," since he observed in the field or in herbaria probable, sometimes obvious, hybrids between this species and *L. intermedia*, *L. Leggettii*, *L. minor*, and *L. villosa*. Putative natural hybrids between *L. racemulosa* and *L. villosa* were also recorded by Wilbur and Daoud.

This genus is perhaps the most distinctive of the Cistaceae because of the minute flowers with three imbricated petals, three essentially sessile plumose stigmas and broad shieldlike placentae, the occurrence of basal shoots, the covering of exclusively simple, falsely bicellular hairs, and the small, nearly globular pollen with a distinctive aperture structure.

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# SYNOPSIS OF THE GENUS ALYSSUM

T. R. DUDLEY

THE FOLLOWING IS A SYNOPSIS of the natural infrageneric groups recognized by the author within the genus *Alyssum* L., of the family Cruciferae. The currently recognized species of *Alyssum* are listed alphabetically, each under its respective section, subsection or series, to provide a convenient source of reference. It is to be noted that sect. SCLEROPTYCHIS Boiss. (1867), which includes *Alyssum creticum* L., and sect. CHRYSITES Schulz (1933), including *Alyssum sinuatum* L., have been omitted from *Alyssum*. These sections and their component taxa are rather to be referred to *Alyssoides* Miller. Section AURINIA (Desv.) Koch (1836) has also been omitted from *Alyssum*. *Aurinia* Desv., which includes the common ornamental *Alyssum saxatile* L., is a genus distinct from Alyssum.

In my recent paper on *Alyssum* (Jour. Arnold Arb. **45**: 57. 1964) may be found citations for the type species and the respective type specimens of most of the infrageneric categories, and also the relevant synonymy. The exclamation mark (!) following the original references to taxa of any rank, indicates that type material of that taxon has been examined.

**Alyssum** Linnaeus, Sp. Pl. 2: 650. 1753; Gen. Pl. ed. 5. 293. 1754.

LECTOTYPE SPECIES: *Alyssum montanum* L. "Habitat in Helvetia" (LINN no. 828:12).[1] (See Britton & Brown, Ill. Fl. No. U.S. ed. 2. 2: 154. 1913; Hitchcock & Green in Internat. Bot. Congr. Cambridge (England), "Nomenclature-Proposals by British Botanists," 171, 1929). — Willd. Linn. Sp. Pl. ed. 4. 3(1): 459. 1800. — DC. Syst. Nat. 2: 301. 1821; Prodr. 1: 160. 1824. — Meyer in Ledeb. Fl. Alt.

[1] Sheet no. 828:12 in the Linnaean herbarium was determined by Linnaeus as "2 montanum." On the back of this sheet Linnaeus wrote "Alyssum fruticosum Alyssum serpyllifolium Amm. e Sibirica & Horto Upsal. 185." This, and the entry in Linnaeus's *Hortus Upsaliensis*, 185. 1748, which reads: "Habitat forte in Siberia, mihi enim enata inter plantas ex seminibus Sibiricus," indicate that the specimen of *Alyssum montanum* cultivated in the Botanic Garden at Uppsala was grown from seed presumably sent to Linnaeus by Amman. I feel that it can be safely stated that these seeds were not collected in "Helvetia" (Switzerland), but rather, from somewhere in Russia, although not necessarily from Siberia as that land area is understood today. The "Helvetia" of *Species Plantarum* no doubt stems from Linnaeus's reference to Bauhin's *Historia Plantarum* 2: 928 *t.* 929. 1650-1651. There is yet another specimen (no. 828:14) of *A. montanum* in the Linnaean herbarium. This specimen was not determined by Linnaeus specifically as *A. montanum*, and as it was not sent by Allioni to Linnaeus until 1757, it could not have served as the basis of the 1753 description. However, that Linnaeus did recognize this specimen as *A. montanum* is shown by the polynomial he wrote on the back of this sheet. This direct quotation from *Hortus Upsaliensis*, 185. 1748, reads: "Alyssum ramulis suffruticosis diffusis foliis punctatis echinatis."

3: 53. 1831; in Ledeb. Fl. Ross. 1: 137. 1842. — Grisebach, Spic. Fl. Rum. & Bith. 1: 274. 1843. — Fenzl in Tchihatcheff, Asie Mineure Bot. 1(3): 294, 296. 1860. — Hook. in Benth. & Hook. Gen. Pl. 1: 73. 1862. — Boissier, Fl. Or. 1: 263. 1867; in Buser, Suppl. Fl. Or. 49. 1888. — Ruprecht, Mém. Acad. St.-Pétersb. VII. 15(2): 98. 1869. — Nyman, Consp. Fl. Eur. 1: 55. 1878; Suppl. Consp. Fl. Eur. 2: 33. 1889. — Halácsy, Consp. Fl. Gr. 1: 88. 1900. — Busch in Kuznetzov, Busch & Fomin, Fl. Cauc. Crit. 3(4): 552. 1909; in Komarov, Fl. U.R.S.S. 8: 340. 1939. — Hayek, Repert. Sp. Nov. Beih. (Prod. Fl. Balc. 1) 30: 428. 1925. — Post in Post & Dinsmore, Fl. Syr., Pal. & Sinai, ed. 2. 1: 82. 1932. — Bornmüller, Repert. Sp. Nov. Beih. (Symb. Fl. Anat.) 89: 46. 1936. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. 17b: 490. 1936. — Rechinger f. Fl. Aegaea, 220. 1943. — Grossheim, Fl. Kavkaza, ed. 2. 4: 211. 1950. — Dudley, Jour. Arnold Arb. 45: 57. 1964.

*Adyseton* Adans. Fam. Pl. 2: 420. 1763 (!). TYPE SPECIES: *Alyssum montanum* L.

*Moenchia* Roth, Tent. Fl. Germ. 1: 273. 1788 (!). TYPE SPECIES: *Alyssum minus* (L.) Rothm.

*Alyssum* sect. *Adyseton* (Adans.) DC. Syst. Nat. 2: 302. 1821 (!).

*Ptilotrichum* Meyer in Ledeb. Fl. Alt. 3: 50. 1831 (!).

*Adyseton* sect. *Disodontea* G. Don, Gen. Hist. Dichl. Pl. 1: 177. 1831 (!). LECTOTYPE SPECIES: *Alyssum montanum* L.

*Koniga* R. Br. sect. *Ptilotrichum* (Meyer) Griseb. Sp. Fl. Rum. & Bith. 1: 278. 1843 (!).

*Alyssum* sect. *Ptilotrichum* (Meyer) Hook. in Benth. & Hook. Gen. Pl. 1: 74. 1862 (!).

DISTRIBUTION: Widespread European and Asiatic genus, mostly south of 50 degrees latitude, with a center of diversity and the greatest number of species in Turkey.

*Plants* annual, or biennial, or if perennial then always with sterile shoots and winter rosettes. *Fertile stems* usually densely foliate. *Indumentum* of stellate hairs with few or many, branched or unbranched rays, often sublepidote or lepidote, occasionally with setae or tuberculate hairs. *Leaves* simple, undivided, entire (sparingly dentate only in *A. homalocarpum*), to about 20 mm. long, bases never swollen or persistent. *Inflorescence* racemose, corymbose, paniculate, umbellate, or rarely candelabriform. *Pedicels* straight and ascending, or divergent and spreading, or flexuose and sigmoid, or deflexed, or arcuate and recurved. *Flower buds* elliptic, longer than broad. *Calyx* elongate. *Sepals* 4, erect, free and monomorphic (or dimorphic and appearing connate because of interlocking indumentum in sect. GAMOSEPALUM), never saccate but often persistent and/or inflated in fruit. *Petals* 4, predominantly yellow, occasionally whitish, or rarely pink-reddish, obovate or spathulate, entire or bilobed, or emarginate or retuse, gradually or abruptly attenuate into claws, occasionally with denticulate claws, and rarely with basal appendages (two species only; *A. pinifolium* and *A. les-*

*biacum*). *Long filaments* 4, unilaterally or bilaterally winged, free, or rarely connate along wing, usually variously toothed and/or appendaged (or wingless, edentate and unappendaged in sect. PSILONEMA). *Short filaments* 2, winged or wingless, usually furnished with connate or free appendages or teeth. *Nectaries* 4, one at each side of short filaments, erect and peglike, or globose, or triangular, or occasionally lobed. *Anthers* elliptic or triangular, introrse, medifixed, obtuse or acute at apex, tip of filaments occasionally prolonged. *Pistils* sessile on receptacle, or rarely short stipitate. *Styles* of various length, slender or stout, often widely dilated to base, persistent. *Silicles* latiseptate, dehiscent or rarely indehiscent, glabrous, or with monomorphic or dimorphic indumentum, rarely papillose or setose, usually held in the same direction as pedicels (except sect. TETRADENIA), bilocular with conspicuous repla, locules 1–6(–8)-ovulate with placentation nearly apical, or distinctly lateral (sect. MENIOCUS); valves compressed, or equally or unequally inflated. *Seeds* winged or wingless, often mucilaginous.

## KEY TO SECTIONS

A. Annual.
  B. Silicles always compressed, glabrous, or with simple setae, and/or papillose (never with stellate hairs), locules 2–4(–8)-ovulate with distinctly lateral placentation. ..... 1. Sect. MENIOCUS.
  B. Silicles always inflated, glabrous, or with monomorphic or dimorphic indumentum, locules always biovulate with nearly apical placentation.
    C. Filaments always slender, wingless, edentate, and unappendaged; petals scarcely longer than sepals. ..... 2. Sect. PSILONEMA.
    C. Filaments always stouter, winged, and/or dentate, and/or appendaged; petals always 1/3–1/2 (or more) longer than sepals. ..... 3. Sect. ALYSSUM p.p.

A. Perennial, or biennial.
  D. Locules always uniovulate. ..... 6. Sect. ODONTARRHENA.
  D. Locules 2–4-ovulate.
    E. Silicles boat-shaped, valves strongly and unequally inflated (one valve convex, the other prominently concave), held horizontally or erect, in opposite direction to pedicels; racemes candelabriform; plants frequently spinose. ..... 5. Sect. TETRADENIA.
    E. Silicles various, but never boat-shaped, valves never as strongly and unequally inflated, held in the same direction as the pedicels; inflorescences various, but never candelabriform; plants never spinose.
      F. Sepals dimorphic, appearing connate because of interlocking indumentum, always persistent in fruit, inner surfaces with indumentum; long filaments always edentate, unappendaged, and closely adjacent, free with overlapping wings, or connate. ..... 4. Sect. GAMOSEPALUM.
      F. Sepals monomorphic, always free, but often persistent in fruit, inner surfaces glabrous; long filaments usually with teeth and/or appendages, always free, and rarely with overlapping wings. ..... 3. Sect. ALYSSUM p.p.

1. Section **Meniocus** (Desv.) Hook. in Benth. & Hook. Gen. Pl. 1: 74 1862. TYPE SPECIES: *Alyssum linifolium* Steph. ex Willd. — Boiss. Fl. Or. 1: 265, 286. 1867. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. **17b**: 492. 1936. — Nyár. Anal. Acad. Rep. Pop. Rom. Secț. Științe Geol. Geog. Biol. ser. A. mem. 3. 1: 7. 1949.

*Meniocus* Desv. Jour. Bot. 3: 173. 1814 (!).

DISTRIBUTION: European and Oriental, with maximum representation in Turkey.

*Plants* annual. *Long filaments* unilaterally winged and toothed. *Short filaments* with free, or basally connate appendages. *Nectaries* globose. *Silicles* dehiscent, glabrous, or with indumentum or simple setae (rarely forked), frequently papillose, locules 2–4(–8)-ovulate with distinctly lateral placentation; valves always compressed. *Seeds* winged or wingless, mucilaginous.

COMPONENT SPECIES:

A. AUREUM (Fenzl) Boiss. Fl. Or. **1**: 286. 1867 (!). Southern and eastern Turkey, Syria, and Israel.

A. BLEPHAROCARPUM Dudl. & Hub.-Mor. Jour. Arnold Arb. **45**: 61. *pl. I, figs. 1–13.* 1964.

A. HETEROTRICHUM Boiss. Diagn. **1**(6): 15. 1845 (!). Iran and Kazakhstan.

A. HUETII Boiss. Fl. Or. **1**: 287. 1867 (!). Endemic to Turkey.

A. LINIFOLIUM Steph. ex Willd. Linn. Sp. Pl. ed. 4. **3**(1): 467. 1800 (!). Common in Europe, North Africa, the Levant, Caucasia, Siberia, and east to India. Naturalized in Australia.

A. MENIOCOIDES Boiss. Ann. Sci. Nat. Paris II. **17**: 158. 1842 (!). Widespread in the Levant, east to Afghanistan.

A. STYLARE (Boiss. & Bal.) Boiss. Fl. Or. **1**: 287. 1867 (!). Endemic to Turkey.

2. Section **Psilonema** (Meyer) Hook. in Benth. & Hook. Gen. Pl. 1: 74. 1862. TYPE SPECIES: *Alyssum dasycarpum* Steph. ex Willd. — Boiss. Fl. Or. 1: 265, 285. 1867. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. 17b: 491. 1936. — Nyár. Anal. Acad. Rep. Pop. Rom. Sect. Științe Geol. Geog. Biol. ser. A. mem. 3. 1: 7. 1949.

*Psilonema* Meyer in Ledeb. Fl. Alt. **3**: 50. 1831 (!).

*Alyssum* subgen. *Tetratrichia* Gay in Cosson, Fl. Atl. **2**: 236. 1885 (!). TYPE SPECIES: *Alyssum granatense* Boiss. & Reut.

*Alyssum* sect. *Eualyssum* subsect. *Hygrochastica* Zohary, Pal. Jour. Bot. Jerusalem Ser. **2**(2/3): 161. 1941 (!). TYPE SPECIES: *Alyssum damascenum* Boiss. & Gaill.

DISTRIBUTION: Europe, North Africa, Egypt, Arabia, the Levant, and east to India.

*Plants* annual. *Filaments* always slender, wingless, edentate, and un-

appendaged. *Nectaries* erect and peglike, or globose. *Silicles* dehiscent, glabrous, or with monomorphic or dimorphic indumentum, held in the same direction as pedicels, and with biovulate locules; valves equally inflated. *Seeds* winged or wingless, mucilaginous.

COMPONENT SPECIES:

A. ALYSSOIDES (L.) L. Syst. ed. 10. 2: 1130. 1759 (!). Widespread in Europe, North Africa, Russia, and east to India. Doubtfully recorded from the Levant. Naturalized in the United States and Canada, and in one locality in Argentina.

A. DAMASCENUM Boiss. & Gaill. Diagn. 3(6): 18. 1859 (!). Syria, Jordan, and Israel.

A. DASYCARPUM Steph. ex Willd. Linn. Sp. Pl. ed. 4. 3(1): 467. 1800 (!). Widespread in eastern Europe, the Levant, Caucasia, and east to India.

A. GRANATENSE Boiss. & Reut. Pugillus. 9. 1852 (!). Spain, Portugal, and North Africa.

A. HOMALOCARPUM (Fisch. & Meyer) Boiss. Fl. Or. 1: 285. 1867 (!). Egypt, Arabia, Iraq, Iran, and Pakistan. Rarely occurring in Syria, Jordan or Israel.

3. Section **Alyssum.** LECTOTYPE SPECIES: *Alyssum montanum* L. — Boiss. Fl. Or. 1: 264, 274. 1867. — Baumgartner, Beil. Jahresb. Nied.-Öst. Land.-Lehrers. Wien.-Neust. 34: xiv. 1907, *ibid.* 36: 1909; Beil. Jahresb. Kaiser Franz Josef-Land.-Gymn. Oberrealsch. Baden bei Wien 48: 1911. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. 17b: 491. 1936. — Nyár. Anal. Acad. Rep. Pop. Rom. Sect. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. 1: 7. 1949.

*Alyssum* sect. *Eualyssum* Griseb. Spic. Fl. Rum. & Bith. 1: 274. 1843. LECTOTYPE SPECIES: *Alyssum montanum* L. (!).

DISTRIBUTION: Europe, North Africa, the Levant, Caucasia, and east to Siberia, Mongolia, and India.

*Plants* annual, biennial, or if perennial then with sterile shoots and winter rosettes. *Sepals* monomorphic, free, but often persistent in fruit; inner surfaces always glabrous. *Petals* predominantly yellow, occasionally pale, and rarely whitish. *Filaments* free, unilaterally or bilaterally winged, and/or dentate, and/or appendaged. *Nectaries* globose or triangular, occasionally lobed, rarely peglike. *Silicles* dehiscent, glabrous, or with monomorphic or dimorphic indumentum, held in the same direction as pedicels, with biovulate locules; valves equally or unequally inflated. *Seeds* winged or wingless, mucilaginous.

COMPONENT SPECIES:

A. AIZOIDES Boiss. Ann. Sci. Nat. Paris, II. 17: 153. 1842 (!). Endemic to Turkey.

A. ARENARIUM Loisel. Fl. Gall. 2: 401. 1807 (!). Seacoasts of southern France and northern Spain.

A. ARGYROPHYLLUM Schott & Ky. Oesterr. Bot. Wochenbl. **7**(29): 229. 1857 (!). Endemic to Turkey.

A. ARMENUM Boiss. Fl. Or. **1**: 278. 1867 (!). Eastern Turkey and the Caucasus.

A. ARTWINENSE Busch in Kuznetsov, Busch & Fomin, Fl. Cauc. Crit. **3**(4): 566. 1909 (!). Endemic to Lazistan (northeastern Turkey and the adjacent Caucasus).

A. ATLANTICUM Desf. Fl. Atl. **2**: 71. *t. 149*. 1798. Spain and North Africa.

A. AURANTIACUM Boiss. Fl. Or. **1**: 276. 1867 (!). Endemic to Turkey.

A. BORNMUELLERI Hausskn. ex Degen, Österr. Bot. Zeitschr. **48**: 108. 1898 (!). Endemic to Turkey.

A. BULBOTRICHUM Hausskn. & Bornm. Mitt. Thür. Bot. Ver. **20**: 3. 1909–1905 (!). Endemic to Turkey.

A. CAESPITOSUM Baumg. Beil. Jahresb. Nied.-Öst. Land.-Lehrers. Wien.-Neust. **36**: 26. 1909 (!). Endemic to Turkey.

A. CALYCOCARPUM Rupr. Mém. Acad. St.-Pétersb. VII. **15**(2): 103. 291. 1869 (!). The Crimea, Caucasia, northern Iran, and Turkish Kurdistan.

A. CANESCENS DC. Syst. Nat. **2**: 322. 1821 (!). Siberia, the Himalayas, and Mongolia.

A. CEPHALOTES Boiss. Diagn. **3**(1): 34. 1853 (!). Endemic to Turkey.

A. CONTEMPTUM Schott & Ky. Oesterr. Bot. Wochenbl. **4**(22): 177. 1854 (!). Widespread in southern and eastern Turkey, and in the Levant to northern Iran.

A. CUNEIFOLIUM Ten. Cat. Pl. Hort. Neap. Append. 58. 1815 (!). Southern Europe.

A. DENSISTELLATUM Dudl. Notes Bot. Gard. Edinb. **24**: 160. *fig. 3, Aa–Ad.* 1962 (!). Endemic to Greece.

A. DESERTORUM Stapf, Denkschr. Akad. Wien. Math. Naturw. **51**: 302. 1886 (!). Widespread in Europe and Asia. Naturalized in Idaho in the United States.

A. DIFFUSUM Ten. Cat. Pl. Hort. Neap. Append. 58. 1815 (!). The Pyrenees, northern Spain, southwestern Alps, and Greece.

A. DOERFLERI Degen, Denkschr. Akad. Wien. Math. Naturw. **64**: 708. *t. 2, figs. 5d–f.* 1897 (!). Northern Greece and southern Yugoslavia.

A. EROSULUM Gennar & Pestal. Mem. Accad. Sci. Torino, II. **16**: 248. 1855 (!). Endemic to Turkey.

A. FASTIGIATUM Heywood, Bull. Brit. Mus. Bot. **1**: 92. 1954 (!). Endemic to Spain.

A. FISCHERIANUM DC. Syst. Nat. **2**: 311. 1821 (!). Southeast Russia, and Siberia.

A. FOLIOSUM Bory & Chaub. Exped. Sci. Morée. 185. *t. 23, fig. 1.* 1832. Greece, Crete, Cyprus, Aegean Islands, and the Mediterranean coast of Turkey.

A. FULVESCENS Sibth. & Smith, Prod. Fl. Gr. **2**: 13. 1813 (!). Aegean Islands, Cyprus, and the Mediterranean coast of Turkey. Recorded doubtfully from Greece.

A. HANDELII Hayek, Beih. Bot. Centr. **45**(2): 1928 (!). Endemic to Greece.

A. HIRSUTUM Bieb. Fl. Taur. Cauc. **2**: 106. 1808 (!). Widespread in southeastern Europe, western Russia, and northern and eastern Turkey.

A. IDAEUM Boiss. & Heldr. Diagn. **2**(8): 35. 1849 (!). Endemic to Crete.

A. IRANICUM Hausskn. ex Baumg. Jahresb. Kaiser Franz Josef-Land.-Gymn.

Oberrealsch. Baden bei Wien **48:** 9. 1911 (!), non Czerniak. (1924). Widespread in the Levant exclusive of Turkey.

A. LANCEOLATUM Baumg. *op. cit.* 11 (!). Iran and Afghanistan.

A. LASSITICUM Hal. Suppl. Consp. Fl. Gr. **2:** 10. 1908 (!). Endemic to Crete.

A. LENENSE Adams, Mém. Soc. Nat. Moscou **5:** 110. 1817. Southeastern Russia and Mongolia.

A. LEPIDOTUM Boiss. Diagn. **1**(1): 73. 1842 (!). Endemic to Turkey.

A. MACROCALYX Cosson & Durand, Bull. Soc. Bot. Fr. **4:** 12. 1857 (!). North Africa.

A. MACROPODUM Boiss. & Bal. Diagn. **3**(6): 18. 1859 (!). Endemic to Turkey.

A. MARGINATUM Steud. ex Boiss. Ann. Sci. Nat. Paris, II. **17:** 157. 1842 (!). Widespread in the Levant, exclusive of Turkey, and extending to southeastern Russia and India.

A. MINUS (L.) Rothm. Repert. Sp. Nov. **50:** 77. 1941. Common in Europe, North Africa, and Asia.

A. MINUTUM Schlecht. ex DC. Syst. Nat. **2:** 316. 1821 (!). Widespread in southeastern and eastern Europe, North Africa, Crete, Cyprus, the Aegean Islands, Turkey, and Syria.

A. MOELLENDORFIANUM Aschers. ex Beck, Ann. Naturh. Mus. Wien **2:** 173. *t. 2, figs. 5–7.* 1887 (!). Yugoslavia.

A. MONTANUM L. Sp. Pl. **2:** 650. 1753 (!). Widespread in Europe, mostly south of 50 degrees latitude.

A. MOURADICUM Boiss. & Bal. Diagn. **3**(6): 16. 1859 (!). Turkey and Lebanon.

A. MUELLERI Boiss. & Buhse, Nouv. Mém. Soc. Nat. Moscou **12:** 6. 1860 (!). Russian Armenia, Caucasus, and northern Iran.

A. MICROPHYLLUM (Meyer) Steud. Nomencl. Bot. ed. 2. **1:** 68. 1841 (!). Siberia.

A. NEVADENSE Wilmott ex Ball & Dudley, sp. nov.[2] Endemic to Spain.

A. OCHROLEUCUM Boiss. & Huet, Diagn. **3**(5): 36. 1856 (!). Endemic to Turkey.

A. OVIRENSE Kerner, Sched. Fl. Exsicc. Austro-Hung. **2:** 99. 1882 (!). Southeastern Alps and western Yugoslavia.

A. PERSICUM Boiss. Ann. Sci. Nat. Paris, II. **17:** 152. 1842 (!). Iran.

A. PRAECOX Boiss. & Bal. in Boiss. Fl. Or. **1:** 275. 1867 (!). Endemic to Turkey.

A. PROPINQUUM Baumg. Beil. Jahresb. Nied.-Öst. Land.-Lehrers. Wien.-Neust. **36:** 22. 1909 (!). Endemic to Turkey.

A. PSEUDO-MOURADICUM Hausskn. & Bornm. ex Baumg. *op. cit.* 6 (!). Endemic to Turkey.

A. PULVINARE Velen. Sitz.-ber. Böhm. Ges. Wiss. Math. Naturw. **33:** 30. 1889 (!). The Balkans.

[2] **Alyssum nevadense** Wilmott ex Ball & Dudley, sp. nov. Holotype, Spain, Sierra Nevada, Almeria, main ridge west of Cerro del Rayo, 25 June 1926, *Wilmott* (BM). Affinis *A. montano* sed habitu humilioris, caulibus minoribus decumbentibus, foliis surculorum sterilium lanceolatis et angustioribus, indumento ex toto valde dense albo-argenteo e pilis stellatis maioribus (0.5–)0.7–1 mm. diametro 5–10 radiatis composito, floribus pallidis minoribus, racemi conferti differt. — Endemic to the Spanish Sierra Nevada. — Sierra Nevada above Minas de Bieres, between Minas de Bieres and Cerro del Rayo, 4 June 1924, *Lofthouse* (BM).

A. PURPUREUM Lag. & Rod. Anal. Ci. Nat. **5:** 275. 1802. Endemic to Spain.
A. REPENS Baumg. Enum. Stirp. Transsilv. **2:** 237. 1816 (!). Widespread in southern and eastern Europe, the Levant, Caucasia, and rarely extending to Iran.
A. ROSTRATUM Stev. Mém. Acad. St.-Pétersb. **3:** 295. *t. 15, fig. 1.* 1809 (!). Southeastern Europe and the Caucasus.
A. SCARDICUM Wettst. Bibliot. Bot. **26:** 24. 1892 (!). The Balkans.
A. SCUTIGERUM Durand, Bull. Soc. Bot. Fr. **4:** 11. 1857. North Africa.
A. SMYRNAEUM Meyer, Bull. Acad. Sci. St.-Pétersb. **7:** 132. 1840 (!). Greece, the Aegean Islands, and Turkey.
A. SPHACIOTICUM Boiss. & Heldr. Diagn. **2**(8): 35. 1849 (!). Endemic to Crete.
A. STAPFII Vierh. Verh. Zool.-Bot. Ges. Wien **64:** 261, *t. 7, fig. 1.* 1914 (!). Widespread in southern and eastern Turkey, the Levant, and east to Afghanistan.
A. STRIBRNYI Velen. Fl. Bulg. 640. 1891 (!). The Balkans, Turkey, Syria, and Lebanon.
A. STRICTUM Willd. Linn. Sp. Pl. ed. 4. **3**(1): 464. 1800 (!). Widespread in the Levant and Caucasia.
A. STRIGOSUM Banks & Sol. in Russell, Natural Hist. Aleppo **2:** 257. 1794 (!). Common in southern and eastern Europe, North Africa, the Levant, and east to Afghanistan.
A. SZOWITSIANUM Fisch. & Meyer, Ind. Sem. Hort. Petrop. **4:** 31. 1837 (!). Common throughout the Levant, east to India.
A. TAYGETEUM Heldr. Verh. Zool.-Bot. Ges. Wien **48:** 703. 1898 (!). Endemic to Greece.
A. TENUIFOLIUM Steph. ex Willd. Linn. Sp. Pl. ed. 4. **3**(1): 460. 1800 (!). Siberia and Mongolia.
A. TRICHOCARPUM Dudl. & Hub.-Mor. Jour. Arnold Arb. **45:** 68. *pl. II, figs. 12–22.* 1964 (!). Endemic to Turkey.
A. TURKESTANICUM Regel & Schmalh. in Regel, Desc. Pl. Nov. Rar. 6. 1882 (!). Transcaspia, Iran, and Afghanistan.
A. UMBELLATUM Desv. Jour. Bot. **3:** 173, 184. 1814 (!). Widespread in the Balkans, Crete, Cyprus, the Aegean Islands, western Turkey, and the Crimea.
A. WIERZBICKII Heuff. Flora **18:** 242. 1835 (!). The Banatus region of Yugoslavia and Romania.
A. WULFENIANUM Schlecht. in Willd. Suppl. Enum. Pl. Hort. Berol. 44. 1813. Southeastern Alps.
A. XANTHOCARPUM Boiss. Ann. Sci. Nat. Paris, II. **17:** 154. 1842 (!). Widespread in Turkey, the Caucasus, northern Syria, and rarely in Lebanon.

4. Section **Gamosepalum** (Hausskn.) Dudl. Jour. Arnold Arb. **45:** 70. 1964. LECTOTYPE SPECIES: *Alyssum lepidoto-stellatum* (Hausskn. & Bornm. ex Hausskn.) Dudl.

*Gamosepalum* Hausskn. Mitt. Thür. Bot. Ver. **11:** 73. 1897 (!). — Schulz, Notizbl. Bot. Gart. Berlin **10:** 109. 1927; in Engler & Prantl, Pflanzenfam. II. **17b:** 494. 1936. — Bornm. Repert. Sp. Nov. Beih. **89:** 58, 59. 1936.

DISTRIBUTION: The Levant, with maximum representation in Turkey.

*Plants* perennial, with sterile shoots. *Sepals* distinctly dimorphic, always persistent, and often inflated in fruit, appearing connate because of interlocking indumentum; inner surfaces with indumentum. *Petals* whitish with purple venation at limb bases, or yellow. *Long filaments* bilaterally winged, edentate and unappendaged, connate, or if free then contiguous with overlapping wings. *Short filaments* with basal, connate appendages or teeth. *Silicles* dehiscent, always with indumentum, held in the same direction as pedicels, and with biovulate locules; valves equally or unequally inflated. *Seeds* narrowly winged or wingless, mucilaginous.

A. Series **Connata** Dudl. Jour. Arnold Arb. **45**: 70. 1964 (!). TYPE SPECIES: *Alyssum lepidoto-stellatum* (Hausskn. & Bornm. ex Hausskn.) Dudl.

DISTRIBUTION: Endemic to Turkey.

*Long filaments* connate. *Indumentum* overall composed of stellate hairs with few, branched rays. *Petals* whitish or pale yellow, with purple venation at limb bases.

COMPONENT SPECIES:

A. LEPIDOTO-STELLATUM (Hausskn. & Bornm. ex Hausskn.) Dudl. *loc. cit.* (!). Endemic to Turkey.
A. PAPHLAGONICUM (Hausskn.) Dudl. *op. cit.* 71 (!). Endemic to Turkey.
A. TETRASTEMON Boiss. Ann. Sci. Nat. Paris, II. **17**: 153. 1842 (!). Endemic to Turkey.
A. THYMOPS (Hub.-Mor. & Reese) Dudl. Jour. Arnold Arb. **45**: 71. 1964 (!). Endemic to Turkey.

B. Series **Libera** Dudl. *op. cit.* 72 (!). TYPE SPECIES: *Alyssum baumgartnerianum* Bornm.

*Long filaments* free, but contiguous with overlapping wings. *Indumentum* overall composed of lepidote hairs with many and branched rays. *Petals* sulphureous, not purple veined.

COMPONENT SPECIES:

A. BAUMGARTNERIANUM Bornm. in Beil. Baumg. Jahresb. Kaiser Franz Josef-Land.-Gymn. Oberrealsch. Baden bei Wien **48**: 16. 1911 (!). Southern Turkey, Syria, Lebanon, Israel, and Iran.
A. CORNINGII Dudl. Jour. Arnold Arb. **45**: 72. *pl. III, figs. 1–11.* 1964 (!). Endemic to Turkey.
A. HARPUTICUM Dudl. *op. cit.* 76. *pl. IV, figs. 1–12* (!). Endemic to Turkey.
A. LYCAONICUM (Schulz) Dudl. *op. cit.* 79 (!). Endemic to Turkey.
A. NIVEUM Dudl. *op. cit.* 78. *pl. III, figs. 12–20* (!). Endemic to Turkey.
A. SULPHUREUM Dudl. & Hub.-Mor. *op. cit.* 74. *pl. IV, figs. 13–26* (!). Southeastern Turkey, and northern Syria and Iraq.

5. Section **Tetradenia** (Spach) Dudley, comb. nov. LECTOTYPE SPECIES: *Alyssum spinosum* L. Sp. Pl. **2**: 650. 1753 (!). TYPE: "Alyssum ramis senilibus spiniformibus nudis" (BM — Hort. Cliff. *Alyssum* no. 1).

*Konig* Adans. sect. *Tetradenia* Spach, Hist. Nat. Vég. Phan. **6**: 492.

*Plants* perennial, often spinose, with sterile shoots and winter rosettes. *Fruiting racemes* candelabriform. *Pedicels* arcuate and recurved. *Petals* white, often pink or reddish. *Long filaments* free, narrowly bilaterally winged, edentate, or with small basal teeth. *Short filaments* with small basal teeth. *Silicles* dehiscent, always glabrous, conspicuously boat-shaped, erect or horizontal, held opposite to the direction of the pedicels, and with biovulate locules; valves strongly and unequally inflated. *Seeds* wingless, not mucilaginous.

COMPONENT SPECIES:

A. COCHLEATUM Cosson & Durand, Bull. Soc. Bot. Fr. **4**: 11. 1857 (!). North Africa.

A. LAPEYROUSIANUM Jord. Obs. Pl. Nouv. **1**: 3. *pl. 1, figs. A1–11.* 1846. The Pyrenees.

A. SPINOSUM L. Sp. Pl. **2**: 650. 1753 (!). Mediterranean Europe, and North Africa.

6. Section **Odontarrhena** (Meyer) Koch, Synop. Fl. Germ. Helv. 59. 1836. LECTOTYPE SPECIES: *Alyssum tortuosum* Waldst. & Kit. ex Willd. — Hook. in Benth. & Hook. Gen. Pl. **1**: 74. 1862. — Boiss. Fl. Or. **1**: 263, 267. 1867. — Nyár. Bul. Grăd. Bot. Cluj **7**: 1, 65. 1927, *ibid.* **8**: 152. 1928, *ibid.* **9**: 1. 1929; Repert. Sp. Nov. **27**: 392. 1930; Bul. Grăd. Bot. Cluj **9**: 69. 1931; Bul. Soc. Ştiinţe Cluj **6**: 446. 1932; Notizbl. Bot. Gart. Berlin **9**: 631. 1932; Bul. Grăd. Bot. Cluj **18**: 82. 1938; Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A, mem. 3, **1**: 1. 1949. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. **17b**: 491. 1936.

*Odontarrhena* Meyer in Ledeb. Fl. Alt. **3**: 58. 1831 (!).

DISTRIBUTION: Widespread in Europe and the Levant, east to Siberia and Afghanistan.

*Plants* perennial, with sterile shoots and winter rosettes, rarely biennial. *Pedicels* rigid, divergent and spreading, or slender, sigmoid and deflexed. *Petals* yellow, usually obovate, rarely with basal appendages. *Long filaments* free, always unilaterally or bilaterally winged, and variously dentate. *Short filaments* always with free or connate appendages, or teeth. *Silicles* dehiscent or indehiscent, glabrous or with indumentum, or rarely papillose, held in the same direction as pedicels or pendulous, and with uniovulate locules; valves equally or unequally inflated, or compressed and undulate

(samaroid and papyraceous in subsect. *Samarifera*). *Seeds* winged or wingless, rarely mucilaginous.

I. Subsection **Inflata** Dudley, Jour. Arnold Arb. **45**: 79. 1964 (!). TYPE SPECIES: *Alyssum tortuosum* Waldst. & Kit. ex Willd.

*Silicles* dehiscent; valves equally or unequally inflated, with inconspicuous venation, never undulate. *Pedicels* divergent and spreading.

DISTRIBUTION: Widespread in Europe and the Levant, east to Siberia and Afghanistan.

COMPONENT SPECIES:

A. ALPESTRE L. Mant. 92. 1767 (!). Central and western Alps.

A. ANATOLICUM Hausskn. ex Nyár. Bul. Grăd. Bot. Cluj **9**: 40. *t. 5 fig. 111; t. 6, fig. 46; t. 7, fig. 56; t. 9, figs. 62 & 63; pl. 29.* 1929 (!). Endemic to Turkey.

A. BAICALICUM Nyár. *Ibid.* **18**: 94. *t. V, fig. 11; fig. 3, no. 3*, 1939. Siberia.

A. BERTOLONII Desv. Jour. Bot. **3**: 172, 185. 1814 (!). Italy and the northwestern Balkans.

A. BORZAEANUM Nyár. Bul. Grăd. Bot. Cluj **6**: 90. 1926 (!). The Balkans and Turkey.

A. BRACTEATUM Boiss. & Buhse, Nouv. Mém. Soc. Nat. Moscou **12**: 18. 1860 (!). Iran and Caucasia.

A. CALIACRAE Nyár. Bul. Grăd. Bot. Cluj **6**: 92. 1926 (!). The Balkans and the Crimea.

A. CALLICHROUM Boiss. & Bal. Diagn. **3**(5): 34. 1856 (!). Endemic to Turkey.

A. CHONDROGYNUM Burtt, Kew Bull. **1949.** 101. *pl. 4.* 1949 (!). Endemic to Cyprus.

A. CONDENSATUM Boiss. & Hausskn. in Boiss. Fl. Or. **1**: 268. 1867 (!). Turkey, Syria, Lebanon, and Iraq.

A. CONSTELLATUM Boiss. Ann. Sci. Nat. Paris, IV. **2**: 244. 1854 (!). Turkey and Iraq.

A. CORSICUM Duby in DC. Bot. Gall. ed. 2. **1**: 34. 1828 (!). Corsica and Turkey.

A. CORYMBOSOIDES Form. Verh. Nat. Ver. Brünn **34**: 329. 1895. The Balkans.

A. CYPRICUM Nyár. Bul. Grăd. Bot. Cluj **7**: 156. *pl. 17; t. 5, fig. 81; t. 8, figs. 136–138.* 1927. Cyprus and Turkey.

A. DAVISIANUM Dudl. Jour. Arnold Arb. **45**: 81. *pl. I, figs. 14 22.* 1964 (!). Endemic to Turkey.

A. DISCOLOR Dudl. & Hub.-Mor. *op. cit.* 80. *pl. V, figs. 1–11* (!). Endemic to Turkey.

A. ERIOPHYLLUM Boiss. & Hausskn. in Boiss. Fl. Or. **1**: 273. 1867 (!). Endemic to Turkey.

A. EUBOEUM Hal. Consp. Fl. Gr. **1**: 93. 1900 (!). Endemic to the Greek island of Euboea.

A. FALLACINUM Hausskn. Mitt. Thür. Bot. Ver. **3–4**: 114. 1893 (!). Greece and Crete.

A. FEDTSCHENKOANUM Busch, Not. Syst. Leningrad **4**: 145. *figs. p. 146.* 1923 (!). Siberia.

A. FILIFORME Nyár. Bul. Grăd. Bot. Cluj **9:** 35. *t. 5, fig. 79; t. 6, fig. 40; t. 7, f. 49; t. 10, f. 53.* 1929 (!). Endemic to Turkey.

A. FRAGILLIMUM (Bald.) Rech. f. Neue Beiträge zur Flora von Kreta. 77. 1943 (!). Endemic to Crete.

A. GEHAMENSE Federov, Not. Syst. Geog. Inst. Bot. Tibilisi, fasc. **10:** 65. *fig. 4.* 1941 (!). Turkish and Russian Armenia.

A. HAUSSKNECHTII Boiss. Fl. Or. **1:** 269. 1867 (!). Endemic to Turkey.

A. HUBER-MORATHII Dudl. Jour. Arnold Arb. **45:** 83. *pl. V, figs. 12–23.* 1964 (!). Endemic to Turkey.

A. INFLATUM Nyár. Bul. Grăd. Bot. Cluj **9:** 43. *t. 5, fig. 113; t. 6, fig. 41; t. 7, figs. 50 & 51; t. 9, figs. 54–58.* 1929 (!). Iran and the Transcaspian.

A. LANIGERUM DC. Syst. Nat. **2:** 308. 1821 (!). Iraq and east to Afghanistan.

A. LIBANOTICUM Nyár. Bul. Grăd. Bot. Cluj **18:** 83. *fig. 1.* 1939 (!). Lebanon.

A. LONGISTYLUM (Somm. & Lév.) Grossh. in Grossh. & Schischk. Scheda Herb. Pl. Or. Exsicc. 18. 1924 (!). Turkish Armenia, Caucasia, and the Crimea.

A. MARKGRAFII Schulz, Ber. Deutsch. Bot. Ges. **44:** 422. *t. VII–VIII, fig. 3.* 1926 (!). Albania and Yugoslavia.

A. MASMENAEUM Boiss. Diagn. **3**(5): 36. 1856 (!). Endemic to Turkey.

A. NEBRODENSE Tineo, Pl. Rar. Sic. Pug. **1:** 12. 1817 (!). Sicily.

A. OBOVATUM (Meyer) Turcz. Bull. Soc. Nat. Moscou **10:** 57. 1837 (!). Southeast Russia, and Siberia.

A. OBTUSIFOLIUM Stev. ex DC. Syst. Nat. **2:** 305. 1821 (!). The Balkans and Russia.

A. OXYCARPUM Boiss. & Bal. Diagn. **3**(5): 35. 1856 (!). Endemic to Turkey.

A. PATERI Nyár. Bul. Grăd. Bot. Cluj **9:** 33. *pl. 26.* 1929 (!). Widespread in Turkey.

A. PENJWINENSIS Dudl. Notes Bot. Gard. Edinb. **24:** 162. *pl. 7 & fig. 4.* 1962 (!). Northern Iraq.

A. POLYCLADUM Rech. f. Phyton **3:** 55. 1951. Iran.

A. ROBERTIANUM Bernard ex Gren. & Godr. Fl. Fr. **1:** 117. 1847 (!). Endemic to Corsica.

A. SERPYLLIFOLIUM Desf. Fl. Atl. **2:** 70. 1798. Southwestern Europe and North Africa.

A. SIBIRICUM Willd. Linn. Sp. Pl. ed. 4. **3**(1): 465. 1800 (!). Widespread in the Balkans, Turkey, the Crimea, and Caucasia.

A. SINGARENSE Boiss. & Hausskn. in Buser, Suppl. Fl. Or. 49. 1888 (!). Iraq.

A. SMOLIKANUM Nyár. Bul. Grăd. Bot. Cluj **9:** 43. *t. 4, figs. 70, 71; t. 6, fig. 54; t. 7, figs. 69–71; t. 9, fig. 71; pl. 30, figs. 2 & 3.* 1929 (!). Greece and Albania.

A. SYRIACUM Nyár. *Ibid.* **18:** 84. *fig. 2.* 1939 (!). Endemic to Turkey.

A. SZARABIACUM Nyár. *op. cit.* 97. *fig. 3, 7; t. 5, fig. 12.* Siberia.

A. TAVOLARAE Briquet, Prod. Fl. Corse **2:** 58. *fig. 1, E; fig. 2, B.* 1913 (!). Mediterranean islands of Tavolara and Sardinia.

A. TORTUOSUM Waldst. & Kit. ex Willd. Linn. Sp. Pl. ed. 4. **3**(1): 466. 1800 (!). Widespread from eastern Europe to Siberia.

A. TROODII Boiss. in Buser, Suppl. Fl. Or. 49. 1888 (!). Endemic to Cyprus.

A. TURGIDUM Dudley, Great Basin Naturalist **24:** 7. *pl. I, figs. A–E, G–K.* 1964 (!). Iran.

II. Subsection **Compressa** Dudley, Jour. Arnold Arb. **45**: 86. 1964. TYPE SPECIES: *Alyssum murale* Waldst. & Kit.

DISTRIBUTION: Southern and eastern Europe, and the Levant.

*Silicles* dehiscent; valves compressed or rarely subinflated, ± undulate, and always conspicuously nerved.

A. Series **Integra** Dudley, Jour. Arnold Arb. **45**: 86. 1964 (!). TYPE SPECIES: *Alyssum murale* Waldst. & Kit.

DISTRIBUTION: Italy, the Balkans, Cyprus, Turkey, Spain, and Jordan.

*Silicles* entire, without marginal wings. *Pedicels* rigid and spreading.

COMPONENT SPECIES:

A. AKAMASICUM Burtt, Kew Bull. **1949.** 100. *pl. 3.* 1949 (!). Endemic to Cyprus.
A. ARGENTEUM All. Miscell. Taur. **5:** 73. 1774. Italy.
A. CASSIUM Boiss. Diagn. **2**(8): 34. 1849 (!). Turkey and northern Syria.
A. JANCHENII Nyár. Preslia **5:** 109. *fig. 1.* 1927 (!). Albania.
A. MURALE Waldst. & Kit. Pl. Rar. Hung. **1:** 5. *t. 6.* 1799 (!). Europe and the Levant.
A. SUBSPINOSUM Dudl. Notes Bot. Gard. Edinb. **24:** 160. *pl. 6.* 1962 (!). Jordan.
A. TENIUM Hal. Consp. Fl. Gr. **1:** 93. 1900 (!). Greece.

B. Series **Crenulata** Dudley, series nov. TYPE SPECIES: *Alyssum crenulatum* Boiss. Diagn. **2**(8): 33. 1849 (!). Holotype, Turkey, D6: Prov. Hatay, in collibus ad radices meridionales jugi Cassii (Akra dağ) in via inter Latakieh et Suadieh, June (May–July) 1846, *Boissier* (G).

DISTRIBUTION: Greece, Turkey, and north Syria.

A serie *Integra* siliculis marginibus alatis crenulatis pedicello capillari flexuoso deflexo suffultis differt.

COMPONENT SPECIES:

A. CILICICUM Boiss. & Bal. Diagn. **3**(5): 34. 1856 (!). Endemic to Turkey.
A. CRENULATUM Boiss. Diagn. **2**(8): 33. 1849 (!). Turkey and north Syria.
A. GIOSNANUM Nyár. Bul. Grăd. Bot. Cluj **7:** 127. *t. 3, figs. 52 & 53; t. 5, fig. 78; t. 8, fig. 102; t. 10, figs. 129–132.* 1927 (!). Endemic to Turkey.
A. HELDREICHII Hausskn. Mitt. Thür. Bot. Ver. **3–4:** 113. 1893 (!). Greece.
**A. pterocarpum** Dudley, nomen novum. *Alyssum elatum* Boiss. & Heldr. Diagn. **2**(8): 33. 1849 (!) — *non* Kreutzer, Anthochron. Pl. Eur. Med. 99, 215. 1840. Lectotype, Turkey. C3: Prov. Antalya, ad rupes portus Tcherali (Çirali) (in campis sterilibus au pied des Montagnes, prés du portus), 13 May 1845, *Heldreich 620* (G); isolectotypes (BM, E, GH, HM, K, OXF, W). Endemic to Turkey.

III. Subsection **Samarifera** Dudl. Jour. Arnold Arb. **45**: 88. 1964. TYPE SPECIES: *Alyssum samariferum* Boiss. & Hausskn.

*Triplopetalum* Nyár. Magyar Bot. Lap. **24**: 97, *fig. p. 98; t. 1, 1–14.* 1925 (!). — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. **17b**: 492. 1936.

DISTRIBUTION: Lesbos, Turkey, and north Syria.

*Silicles* indehiscent, samaroid, papyraceous, undulate, pendulous, always compressed. *Pedicels* slender, flexuose, and deflexed. Seeds mucilaginous.

COMPONENT SPECIES:

A. CARICUM Dudl. & Hub.-Mor. Jour. Arnold Arb. **45**: 89. *pl. II, figs. 1–11.* 1964 (!). Endemic to Turkey.

A. DUBERTRETII Gombault, Mém. Soc. Bot. Fr. **33**: 4. 1952. Endemic to Turkey.

A. FLORIBUNDUM Boiss. & Bal. Diagn. **3**(5): 33. 1856 (!). Endemic to Turkey.

A. LESBIACUM (Candargy) Rech. f. Fl. Aegaea, 226. 1943. Endemic to the Greek island of Lesbos.

A. PELTARIOIDES Boiss. Ann. Sci. Nat. Paris II. **17**: 158. 1842 (!). Endemic to Turkey.

A. PINIFOLIUM (Nyár.) Dudl. Jour. Arnold Arb. **45**: 92. 1964 (!). Endemic to Turkey.

A. SAMARIFERUM Boiss. & Hausskn. in Boiss. Fl. Or. **1**: 272. 1867 (!). Turkey and north Syria.

A. TRAPEZIFORME Bornm. ex Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A, mem. 3, **1**: 83. *t. 1, fig. 1; t. 6, figs. 4–6.* 1949 (!). Endemic to Turkey.

A. VIRGATUM Nyár. Bul. Grăd. Bot. Cluj **7**: 115. *pl. 10, t. 4, figs. 60–62; t. 6, fig. 61; t. 7, fig. 92.* 1927 (!). Endemic to Turkey.

## SPECIES NON SATIS NOTAE

*A. americanum* Greene, Pittonia **2**: 224. 1892 (!). The Yukon in North America. Porsild (Rhodora, **41**: 239. 1939 and Natl. Mus. Canada Bull. **121**: 202. 1951) accepts this species as the only indigenous American representative of the genus. Following Porsild, Anderson, in his *Flora of Alaska*, 267. 1959, lists *Alyssum americanum*. However, although Hultén (Lunds Univ. Årksskr. II. Sect. 2. **41**(1): 886. 1945) maintains the binomial, he claims that it agrees exactly with Siberian plants which have been known by a number of authors as "*A. alpestre*" or "*A. sibiricum*." In 1939, Busch applied a *nomen novum*, *A. biovulatum* (see below), to refer to the Siberian plants; but if the plants from the Yukon and Siberia are conspecific, *A. americanum* is an earlier name and must be used. Busch (1939) states that his *A. biovulatum* is a new name for that which he described, discussed, and illustrated in detail as *A. sibiricum* in his *Flora Siberiae et Orientis Extremi* **6**: 550–552. 1931. In this work Busch cites as a synonym of "*A. sibiricum*," *Odontarrhena obovata* Meyer ( = *Alyssum obovatum* (Meyer) Turcz.). If in fact, *A. americanum*, *A. biovulatum*, and *A. obovatum* are the same species, *A. obovatum* must be used as the correct

epithet. I have examined the holotype and isotypes of *A. americanum*, which agree in most characters with material of *A. obovatum*. I feel, however, that the question of whether the name *A. americanum* should be maintained for an indigenous outlier of an entirely Old World genus should be left open until more specimens (as *A. obovatum*, or *A. biovulatum*, or "*A. sibiricum*") from the Kamchatka and Yakutsk provinces in Siberia have been carefully compared with the plants from the Yukon.

*A. antiatlanticum* Emb. & Maire, Bull. Soc. Hist. Nat. Afr. Nord **23:** 165. 1932. North Africa. This plant is put in sect. PSILONEMA because the petals are only slightly longer than the sepals and the glands are erect and peglike. The fruits, however, are described as being cochleate and glabrous, and the plant is a suffrutescent perennial. Perennials are, to date, unknown in sect. PSILONEMA, as are fruits similar to those of *A. spinosum* or *A. cochleatum* (both in sect. TETRADENIA). In the diagnosis of *A. antiatlanticum* it is stated that the species is allied to *A. cochleatum* and *A. montanum* (sect. ALYSSUM). As type material of *A. antiatlanticum* has not been examined, it is impossible from the description to say whether it is a good species or possibly a synonym of another, such as *A. cochleatum*.

*A. biovulatum* Busch in Komarov, Fl. U.R.S.S. **8:** 346. 1939. Siberia. See notes above under *A. americanum*.

*A. brughieri* Colla, Herb. Pedem. **1:** 142. 1833. Italy. No judgement can be made about this name without examination of the type in hb. Biroli (TO). In the description, however, Colla allies it to *A. argenteum*, of which it may well be a synonym.

*A. costei* Sennen & Pau, Bull. Acad. Geog. Bot. **18:** 453. 1908. Spain. According to the description, this plant is related to *A. lapeyrousianum* (sect. TETRADENIA), of which it may be a synonym. However, until the type material is studied, it is not possible to place this name in the correct section.

*A. djurdjurae* Chod. Bull. Soc. Bot. Fr. **36:** 19. 1889. North Africa. This species is assigned to sect. ALYSSUM, but is described as being morphologically intermediate between *A. atlanticum* (sect. ALYSSUM) and *A. serpyllifolium* (sect. ODONTARRHENA). The characters noted in the description appear to agree with *A. atlanticum*, but before examining the type material no judgement should be made.

*A. emarginatum* Zahl ex Vis. Fl. Dalm. **3:** 117. 1852. Yugoslavia. It is claimed that this species is intermediate between the perennial *A. montanum* and the annual "*A. campestre*" ( = *A. minus*). The fruits are described, however, as being glabrous. Type material must be examined before a decision is made concerning the application of this name.

*A. embergeri* Quezél, Bull. Soc. Sci. Nat. Maroc **31:** 254. 1951. North Africa. According to the description this plant is allied to *A. montanum* and *A. flahaultianum* (see below), but it is impossible to tell from the description alone whether it should be maintained as a distinct species. The description appears to fit *A. atlanticum*.

*A. filifolium* Wahlenb. in Berggren, Resor. i. Europa och Österländerna Bih.

**2**: 54. 1826. ? Asia Minor. The original reference for this name has not been seen; however, an account of Jacob Berggren's journey, by Wahlenberg, appeared in *Isis von Öken* **21**: 971–1006. 1828. There is on page 990 of this work a description of *A. filifolium* by Wahlenberg. Although in *Index Kewensis* **1**: 97. 1895, this plant is cited from Asia Minor, Wahlenberg states that it was collected by Bergren [one g] in "Morgenland." Until the type is studied (SBT) the name should not be used. The description in *Isis von Öken* could apply to any annual with glabrous fruits in *Alyssum*.

*A. flahaultianum* Emb. Bull. Soc. Sci. Natur. Maroc **15**: 199. 1935. North Africa. This plant is described as a perennial in sect. ALYSSUM, allied to *A. serpyllifolium* (sect. ODONTARRHENA), having rose colored flowers, glabrous subcochleate fruits, and few-fruited racemes, characters which seem to apply better to *A. cochleatum* (sect. TETRADENIA). Judgement must be reserved, however, until the type material has been seen.

*A. globosum* Grossh. Izv. Azerbaidzh. Fil. Ak. Nauk. S.S.S.R. **5**: 74. 1939. Caucasus. The original publication of this species is apparently unavailable in the United States or Great Britain, so application of the name must wait.

*A. hakaszkii* Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. **1**: 32. 1949. Siberia. See *A. subbaicalicum* below. This species is described as being "sp. trans. n. = *A. microphyllum–obovatum*" and may be a synonym of either.

*A. heideri* Kroch. Suppl. Fl. Silesia **4**(2): 168. 1823. Germany. The information in the description of this plant is inadequate to place it in any section of *Alyssum*.

*A. "muricatum* mihi vel *tuberculatum"* Kit. Linnaea **32**: 498. 1863. Hungary. Kitaibel evidently could not make up his mind as to an appropriate specific epithet for this taxon, and supplied two names. Although he allies it to *A. sibiricum*, the description of this annual compares favorably to *A. alyssoides*. However, a decision should not be made until the type material has been examined.

*A. odoratum* Colla, Herb. Pedem. **1**: 141. 1833. Italy. There are no species of *Alyssum* with scented flowers as this specific epithet suggests. It is impossible to tell from the description, and without examining the type specimen (TO, hb. Bellardi), whether the name applies to *Alyssum* or if it should be referred to another genus, for example, *Lobularia* (*Lobularia maritima*, the "Sweet Alyssum" having highly scented flowers).

*A. subbaicalicum* Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. **1**: 18. 1949. Siberia. The holotype of this species was collected in Siberia in the district Hakaszki. It is probably synonymous with *A. hakaszkii*, but the descriptions being inadequate, do not offer much assistance. Of interest is that the type of *A. subbaicalicum* was collected by *Golubincev*, and is deposited in the University of Tomsk herbarium (TK). One of the specimens cited as *A. hakaszkii* (see above) was also collected by *Golubincev*, deposited in the same herbarium, and may well be a duplicate. *Alyssum subbaicalicum* is described as being "sp. trans. n. = *A. baicalicum–microphyllum*" and may be a synonym of either taxon, both of which are apparently good species.

# COMPARATIVE ANATOMY OF THE LEAF-BEARING CACTACEAE, XII
## PRELIMINARY OBSERVATIONS UPON THE STRUCTURE OF THE EPIDERMIS, STOMATA, AND CUTICLE

I. W. BAILEY [1]

THE TAXONOMIC SIGNIFICANCE OF structural variations in stomatal apparatuses [2] was strongly emphasized by Solereder (1899). Following the earlier work of Prantl (1872), Vesque (1889) and others, he distinguished a number of significant structural types, e.g., rubiaceous, false rubiaceous, cruciferous, caryophylleous. In the rubiaceous types (paracytic forms of Metcalfe and Chalk, 1950) the stomata are accompanied on either side by one or more accessory cells oriented parallel to the long axis of the pore and guard cells. In the true rubiaceous type the subsidiary cells are derived from the same mother cell as the guard cells; whereas in the false rubiaceous forms the accessory cells arise by secondary divisions in neighboring epidermal cells. Since the publication of Strasburger's (1866–67) paper, the Cactaceae have been regarded by later investigators as having stomatal apparatuses of the true rubiaceous form.

In securing stems of varying sizes and ages preserved in formalin-acetic-alcohol (as a basis for investigations of the xylem reported upon in preceding papers of this series), younger stems bearing leaves were usually included in collections of *Pereskia*, *Pereskiopsis* and *Quiabentia*. Such collections are difficult to obtain and have involved the active cooperation of many botanists. Young stems and leaves being thus available, it seemed advisable to initiate preliminary investigations, not only of stomata, but also of the epidermis and cuticle.

The leaves of the three genera now available to me commonly have two, three, or four thin walled, crescent shaped subsidiary cells oriented parallel to the guard cells of the stomata (FIGS. 1–4). At times there is but one subsidiary cell and at others secondary transverse divisions may occur in one or more of the subsidiary cells. Infrequently, in aberrant leaves some of the stomata appear to have no accessory cells derived from the same mother cell as the guard cells.

The thin walled, crescent shaped accessory cells appear at least superficially to be derived from the same mother cell as the guard cells, in conformity with Strasburger's conclusion based upon detailed developmental

[1] This investigation was financed by a grant from the National Science Foundation. I am indebted to the American Philosophical Society for the loan of a Wild microscope.

[2] In this paper stoma and stomata are used in referring to a pair of guard cells and the aperture between them, stomatal apparatus where subsidiary or accessory cells are involved in addition.

investigations of stomata in *Pereskia aculeata* Mill. and other cacti. Such an interpretation is strengthened by the not infrequent occurrence of groups of four or more thin walled, slender cells oriented parallel to each other, but not having completed differentiation of guard cells and an aperture between them.

As seen in surface views, the size and number of the stomata and the number and transverse diameter of the crescent shaped subsidiary cells varies more or less markedly in different leaves of the same taxon, in different leaves of the same plant, and in different parts of the same leaf. Similar forms of stomatal apparatuses occur in the epidermis of young stems.

The size, form, and orientation of epidermal cells is highly variable in the three genera. At times the anticlinal walls of the cells are smooth (FIGS. 2 and 4), whereas in other cases they are conspicuously undulating (FIG. 3). The stomatal apparatus may be jacketed by epidermal cells of but slightly modified size and form (FIG. 3). They may be completely (FIG. 1+), or partly (FIG. 4) jacketed by a pair of epidermal cells whose longer curved axis is oriented parallel to that of the guard cells and subsidiary cells. One or both of these curved epidermal cells may have secondary transverse divisions (FIG. 2). Where the pair of epidermal cells does not completely jacket the stomatal apparatus, one, two or more conspicuously small epidermal cells oriented at right angles to the major axis of the guard cells may be present (FIG. 4+). In some cases the stomatal apparatus tends to be jacketed by a ring of small epidermal cells. In other cases the stomatal apparatus is situated in a broadened complex of small epidermal cells (FIG. 12).

Owing to variations in the breadth of subsidiary cells and their tendency to divide transversely at times, and to variations in the size, form, and orientation of epidermal cells which jacket the stomatal apparatuses, it is difficult in some cases — without developmental evidence — to determine with certainty which accessory cells arise from the same mother cell as the guard cells. Furthermore, owing to the wide ranges of structural variability of the epidermis and stomatal apparatuses within a taxon, morphological criteria for differentiating taxa are of uncertain reliability unless based upon very extensive collections of leaves and young stems from plants of different ages when grown under varying environmental influences. However, the cuticle, epidermis, stomata, and sub-epidermal layers of available material, when studied in adequately stained periclinal and anticlinal sections, appear to provide potentially useful criteria in the comparison of different categories of *Pereskia*, and in distinguishing the genus from *Pereskiopsis* and *Quiabentia*. In addition, such investigations are particularly desirable from a physiological point of view in regard to the structure and functioning of stomata, and in studying the conservation of moisture in leaves and in young stems prior to periderm formation.

As shown in the second paper of this series (Bailey, 1961a), *Pereskia sacharosa* Griseb., *P. grandifolia* Haw., *P. bleo* DC., *P. moorei* Britt. & Rose, *P. tampicana* Web. and *P. corrugata* Cutak belong in a distinct

category of pereskias characterized by having consistently occurring forms of aggregated fiber-sclereids in their secondary phloem. Their xylem exhibits less divergent trends of specialization than that of other pereskias (Bailey, 1962, 1963c). In this category of taxa, having large, thin, pinnately veined leaves, stomata are at times few in number or absent on the upper or adaxial surface of the foliar appendages.

When epidermal peels are stained in sudan III or in sudan III and Haidenhein's haematoxylin and mounted in glycerin, the cuticle and the outer periclinal wall of the epidermal cells either exhibit no conspicuous structural patterns (FIG. 1), or have variously oriented striations (FIG. 5). In view of the emphasis that has been placed upon cuticular striations in taxonomic investigations it is essential to determine whether such striations are present in unmodified living leaves or are produced by differential contractions of the cuticle and epidermal walls during fixation, dehydration, and other treatments. In the pereskias discussed in the preceding paragraph, cuticular striations, when present, are not due primarily to inequalities in thickness of the cuticle but to contractions of a cuticle of relatively uniform thickness forming folds or ridges. It is significant in this connection that in unlignified, unsuberized and uncutinized meristematic and other tissues of plants the primary walls contract markedly during dehydration. Furthermore, adjacent tissues in intact plants not infrequently are under differential tensions which may be released or modified in peels or sections of leaves producing morphological changes even prior to dehydration. Where cuticular striations occur, the primary walls of the epidermal cells are smooth except for the outer surface of the outermost walls which have projections or ridges corresponding to the folds in the cuticle.

In *Pereskia sacharosa* and allied taxa the cuticular striations, when present, vary markedly in form and orientation, not only in different leaves of the same taxon or plant, but also in different parts of a single leaf. At times, they may be linear and parallel to one another and may extend from cell to cell particularly in axially elongated cells overlying the midvein. They may be radially oriented in relation to the stomata or some particular cell of the epidermis (FIG. 5). In other cases they may be variously convoluted and oriented. The variations in pattern appear to be correlated with variations in the size, form, and orientation of the epidermal cells and to the thickness and degree of contraction of primary walls during dehydration. The range of variability is so extensive as to render difficult and laborious any attempt to differentiate species upon the basis of such diagnostic criteria. It should not be inferred from this, however, that even where cuticular striations are induced by dehydration in other families, differences in the presence or absence of such structures may not be due to consistent differences in the cellular structure and behavior of the leaves in related species.

In the leaves of the category of pereskias under discussion, the outer cells of the mesophyll are relatively large and thin walled (FIG. 7). The stomata are subtended by intercellular spaces of irregular ramifying form

in the chlorenchymatous tissue. As seen in median sectional view, the more or less circular guard cells have thickened walls on their upper and lower surfaces. The first pair of subsidiary cells are thin walled and their internal extensions curve about the guard cells exhibiting various degrees of approximation. The relatively thin part of the cuticle overlying the stomatal apparatus curves inwardly into the frontal cavity forming slender outer "ledges" but commonly more slender than those illustrated in FIG. 15. Very tenuous extensions of the cuticle pass inwardly lining surfaces of the aperture but without forming conspicuous internal ledges as in some dicotyledonous plants. Inner extensions of the tenuous cuticle may likewise occur on the exposed surfaces of cells in the subtending intercellular cavity of the mesophyll.[3] It appears likely that in the above category of stomatal apparatuses closure of the stomata may result (1) by contact between the outer cuticular ledges, (2) by contact between the guard cells, and (3) by approximation of the inner parts of the first-formed pair of subsidiary cells, as in (FIG. 7).

In vigorous, rapidly elongating shoots, periderm formation is retarded; in the case of internodes, appearing first in parts at a considerable distance below the apex of a stem. The lower internodes have a markedly thickened cuticle and massive, wedge shaped accumulations of cutin which extend inward between the epidermal cells (FIG. 16).[4] Although the cells of the outer cortex tend to be smaller, no collenchymatous outer layers or crystalliferous hypodermis are formed, as noted in the third paper of this series (Bailey, 1961b). Stomata are of sporadic and relatively infrequent occurrence, particularly in *P. sacharosa*, being absent in some internodes or parts of them. Where stomatal apparatuses are present, the walls of their cells are very thin (FIGS. 11 & 12), and the part of the cuticle which overlies them is tenuous. Furthermore, the cuticular ledges lining the entrance to the aperture are slender as in the case of leaves.

The genera *Pereskiopsis* and *Quiabentia* differ from this and other categories of *Pereskia* in having no characteristic forms of sclereids in their secondary phloem. In addition, the genera differ from this category of pereskias, in having highly advanced trends of divergent specialization in their xylem (Bailey, 1964). When epidermal peels of the comparatively thick, palmately or pseudo-palmately veined leaves are obtained, and are subjected to the same treatments and staining as those from the thin, pinnately veined leaves of the preceding pereskias, epidermal cells (with the exception of those of the stomatal apparatus) exhibit more or less conspicuous punctate or reticulate patterns of varying degrees of coarseness (FIGS. 2 & 4). At times cuticular striations are visible in addition. In anticlinal sections, these outer primary walls have a beaded appearance suggestive of inequalities in thickness. In surface views, the more intensive staining of parts of the reticulate patterns in haematoxylin suggests the

[3] For clarification of nomenclature and a general discussion of the structure of stomata see Esau (1953).

[4] From a strictly developmental, rather than a purely descriptive, point of view the thickening probably progresses largely from within outwardly.

possibility of differences in chemical composition. The structure of these walls obviously merits more detailed and comprehensive investigation since it may ultimately provide a significant criterion in differentiating leaves of *Pereskiopsis* and *Quiabentia* from those of *Pereskia*. All material available to me at present was preserved in F.A.A. It is essential to determine to what extent the reticulate patterns may have been induced or exaggerated by contractions due to dehydration as in the case of cuticular striations.

The leaves of *Pereskiopsis* and *Quiabentia* usually have abundant stomata on their upper as well as their lower surface. The cuticle overlying the epidermal cells tends to be of relatively uniform thickness except where it forms more or less massive accumulations above the central part of the guard cells and at times between the guard cells and subsidiary cells (compare FIGS. 17 & 18). These thicker parts of the cuticle deform the guard cells and depress them inwardly. In extreme cases, the central parts of the guard cells are greatly reduced in diameter (FIG. 18). This is in marked contrast to what occurs in the stomata of the pereskias discussed on preceding pages, where the cuticle merely forms slender ledges lining the entrance to the stomatal aperture.

These structural differences are strikingly demonstrated in anticlinal sections of young stems (FIGS. 17 & 18) which have numerous stomatal apparatuses, and in surface views of the epidermis when intensely stained in sudan III (FIG. 13). In the case of the pereskias, the thick cuticle forms massive intercellular intrusions between the cells of the epidermis except in the stomatal apparatuses (FIGS. 11 & 12). On the contrary, in young stems of *Pereskiopsis* and *Quiabentia* massive intrusions of the cuticle are largely confined to the stomatal apparatuses (FIG. 13).

It should be emphasized in these connections that it is essential in dealing with young stems to compare internodes in as nearly equivalent stages of development as possible, particularly those which have completed or nearly completed elongation prior to periderm formation. This is due to the fact that significant changes may occur in the cuticle, and in the cells of the epidermis and sub-epidermal layers during early stages of the elongation and increase in circumference of young stems. Similarly in dealing with leaves, changes in thickness of the cuticle, in the form of epidermal cells, and in the internal structure of stomata may occur during successive stages of the expansion and maturation of leaves. Furthermore, it should be kept in mind that unusually thin small leaves of shoots grown under certain environmental influences may vary more or less markedly in structure from larger thicker leaves of plants grown in different environments. This may account at least in part for the structural discrepancy between FIG. 3 (leaf from a rapidly elongating shoot in a greenhouse) and FIG. 6 (leaf from the slower growing branch of an old tree in its native habitat).

In sectional views of leaves and young stems of *Pereskia sacharosa* and allied taxa, the first pair of subsidiary cells commonly does not extend inwardly in excess of the general thickness of the epidermis (FIG. 7), whereas in the case of *Pereskiopsis* it is usually more extensive internally

(Figs. 17 & 18). However, in both cases the innermost parts of the first pair of subsidiary cells exhibit varying degrees of approximation when not actually in contact, as in Fig. 7.

Young stems of *Perekiopsis* and *Quiabentia*, in contrast to those of the pereskias, are characterized by having collenchymatous layers and a well developed crystalliferous hypodermis subtending the epidermis (Bailey 1961b). This taxonomically and physiologically significant difference in structure is illustrated in Figs. 14 & 19. Where collenchymatous layers are formed (Fig. 19) there are no intercellular spaces in the tissue except in clearly defined channels subtending the stomata. These channels communicate internally with intercellular spaces in the subtending, large, thin walled, chlorenchymatous tissue. They are jacketed by unpitted parts of the walls of collenchymatous cells (Fig. 22), and in turn by very tenuous intrusions of the cuticle, so tenuous as not to be visible in Fig. 22.

In young stems of *Pereskiopsis* and *Quiabentia*, the numerous, more or less closely aggregated druses of the hypodermal layer are compact and rotund (Fig. 20) and commonly differ from the diffusely distributed ones of the inner cortex which tend to be of stellate form (Fig. 21). During development of the crystalliferous hypodermis, enlargement of the crystals presses the epidermal cells outwardly and laterally, thus more or less drastically modifying their form and arrangement. Not infrequently the druses press laterally into the intercellular channels subtending the stomata and at least partly occlude their entrances.

Anatomically more specialized species of *Pereskia* exhibit less consistent differences in distinguishing the genus from *Pereskiopsis* and *Quiabentia*. In the case of *P. aculeata* Mill. and such Peruvian and Bolivian pereskias as *P. humboldtii* Britt. & Rose, *P. weberiana* Schum., and *P. diaz-romeroana* Cárd. (which have markedly divergent trends of specialization in their xylem, Bailey, 1962, 1963a) there is a tendency for the outer cortical layers in young stems to become conspicuously thicker-walled and to appear at least pseudo-collenchymatous. Furthermore, although no typical crystalliferous hypodermis is formed, there is a tendency for relatively widely spaced, often linearly arranged aggregations of rotund druses to occur in the outermost layer of the cortex. Such occurrences are at least suggestive of possible initial trends of specialization which become exaggerated and dominant in *Pereskiopsis* and *Quiabentia*.

The stomata in normally developing leaves of these taxa have cuticular ledges resembling those of *Pereskia sacharosa* and allied taxa. However, young stems have consistently more numerous stomata than do those of the primitive category of pereskias. The lowermost internodes of the Andean pereskias prior to periderm formation tend to have a thick cuticle and massive intercellular accumulations of cutin intruding between the epidermal cells as in *P. sacharosa* and allied taxa, but they have more extensive deposits of cutin overlying the guard cells and accessory cells as in *Pereskiopsis* and *Quiabentia* (Fig. 13). In the case of *P. aculeata* periderm formation is so precocious in young shoots that I have not succeeded in obtaining internodes bearing stomata in stages of elongation and

increase in circumference comparable to those available in collections of the Andean pereskias. In younger developing internodes of *P. aculeata* the cuticle is thin and jackets a conspicuously papillose outer surface.

As shown in the first paper of this series (Bailey, 1960), *Pereskia pititache* Karw. (*P. conzattii* Britt. & Rose), *P. autumnalis* (Eichlam) Rose and *P. nicoyana* Web. differ from the pinnately veined pereskias in having palmate or pseudo-palmate venation comparable to that which occurs in *Pereskiopsis* and *Quiabentia*. However, the divergent trends of specialization in the xylem of these taxa are less advanced than in *P. aculeata* and the Andean pereskias (Bailey, 1963b). The cuticle overlying the epidermal cells may be smooth (FIG. 3) or it may have contraction folds, i.e., cuticular striations (FIG. 6) comparable to those that occur in other pereskias. The stomatal apparatuses in surface views of leaves vary markedly in form in the three taxa. In thick, fully expanded leaves from trees growing in the wild, the stomata differ from those of previously discussed categories of pereskias in having massive accumulations of cutin overlying the guard cells, as in *Pereskiopsis* and *Quiabentia*. Periderm formation is so precocious in young shoots of these pereskias that Dr. Boke and I have not succeeded as yet in obtaining material adequate for determining whether similar stomata occur in stems. However, since the cork cambium of cacti commonly arises by periclinal divisions in the epidermis, it is possible to observe after periderm formation is initiated that no collenchymatous layers or crystalliferous hypodermis are formed in young stems of the three pereskias.

In the case of *Pereskia colombiana* Britt. & Rose, *P. guamacho* Web., *P. cubensis* Britt. & Rose and *P. portulacifolia* Haw. adequate collections of roots and stems were obtained for studying divergent trends of specialization in the xylem (Bailey 1963d). Unfortunately only a few collections of leaves and young stems have been obtainable thus far. Available evidence at present suggests, however, that the stomatal apparatuses of these taxa not only have slender cuticular ledges, but also accumulations of cutin penetrating between the guard cells and subsidiary cells. These deposits of cutin are much less massive than those which occur in the preceding category of pereskias and in *Pereskiopsis* and *Quiabentia*. Stomata are of infrequent occurrence in the epidermis of young stems, thus resembling the situation in *P. sacharosa* and allied taxa, but the cuticles are thin and devoid of massive intercellular intrusions of the epidermis. The stems are devoid of collenchymatous layers and a crystalliferous hypodermis.

## DISCUSSION AND CONCLUSIONS

In preceding papers of this series I have shown that *Pereskiopsis* and *Quiabentia* may be differentiated anatomically from *Pereskia* by (1) the characteristic development in young stems of a highly specialized crystalliferous hypodermis in these genera (Bailey, 1961b), by (2) the absence of diagnostic forms of sclereids in their secondary phloem (Bailey, 1961a),

and except in comparisons with *Pereskia pititache*, *P. autumnalis* and *P. nicoyana*, by (3) the characteristic palmate or pseudo-palmate vasculature of their leaves (Bailey, 1960). In addition, I have shown on preceding pages that, except in comparison with stems of *Pereskia aculeata* and the Andean pereskias, *Pereskiopsis* and *Quiabentia* are characterized by having typical collenchymatous outer cortical layers.

A preliminary investigation of cuticles, epidermal cells, and stomatal apparatuses reveals such wide ranges of variability within taxa, particularly in superficial views of stomatal apparatuses, as to be of questionable taxonomic reliability unless based upon very extensive collections of material from plants of different ages when grown under different environmental influences. However, detailed investigation of periclinal and anticlinal sections of available leaves and young stems reveals some structural differences of apparently potential taxonomic significance. The occurrence of punctate and reticulate structures in the outer periclinal walls of epidermal cells in leaves of *Pereskiopsis* and *Quiabentia* may eventually provide a useful criterion in differentiating the foliar appendages of these genera from those of *Pereskia*. Furthermore differences in thickness of the cuticle, in intercellular accumulations of cutin between cells of the epidermis, and in the deposition of cutin in the frontal cavity or vestibule of stomatal apparatuses have at least supplementary significance in differentiating certain categories of *Pereskia*, and in separating one or two of them from *Pereskiopsis* and *Quiabentia*.

It should be emphasized again in this connection that investigations of the cuticle, epidermis and stomatal apparatuses, and of the subtending outer cortical layers of young stems prior to periderm formation are particularly desirable from a physiological point of view, i.e., in regard to the functioning of stomata, and in retention of moisture in leaves and young stems of plants growing in semi-arid or arid environments.

In the case of *Pereskia sacharosa*, *P. grandifolia* and allied taxa, stomata frequently are few in number or absent on the upper surface of the relatively large thin leaves, and on the surfaces of internodes of young stems prior to periderm formation which tends to be more or less precocious in its development. The stomatal apparatuses, even on the under surfaces of the leaves, exhibit no conspicuous structural modifications for the prevention of water loss such as occur in many dicotyledons growing in arid environments. This may be due at least in part to the abscission of leaves at the end of a rainy season. Although the internodes of young stems prior to periderm formation have very thick cuticles and massive intercellular accumulations of cutin between the epidermal cells (which may have some physiological significance during the dry season), the cuticle overlying the stomatal apparatuses is tenuous, and there are no conspicuous structural adaptations for the prevention of loss of moisture. If the stomata are actually functional, as seems questionable in some cases, regulation of moisture probably is controlled merely by the opening and closing of the stomatal aperture.

In the case of *Pereskiopsis* and *Quiabentia* and such pereskias as *P.*

*pititache* and allied taxa, the massive accumulations of cutin in the stomatal apparatuses of fully matured leaves prior to abscission, and in the fully elongated internodes of young stems shortly prior to periderm formation raises important physiological questions regarding the functioning of stomata in these plants. In such stomatal apparatuses as those illustrated in FIGS. 17 and 18 it appears unlikely that the stomata can be fully functional even where the guard cells contain vestiges of viable protoplasts. In certain of my collections the guard cells of some or all of the adjacent stomatal apparatuses have collapsed and are thoroughly impregnated with cutin (FIG. 9). It is of interest in this connection that some of the druses in fully matured cells of the crystalliferous hypodermis may be partly or completely jacketed by cutin.

In general in the leaf-bearing Cactaceae the ordinary epidermal cells appear to be devoid of chloroplasts, but where the stomata appear to be potentially functional with partly or fully open apertures, the guard cells, and sometimes the subsidiary cells are packed with green plastids (FIG. 8). This raises the question whether stomata which are functional during earlier stages of the development of leaves and young stems subsequently become occluded and incapable of functional activity as in FIG. 9. In some taxa the epidermis is in direct contact with subtending thin walled chlorenchymatous tissue, whereas in young stems of some taxa it is separated from such tissue by layers of thick walled collenchymatous cells. The collenchymatous tissue, like the epidermis, contains few if any chloroplasts and, since it is devoid of intercellular spaces, must retard the movement of gases and water vapor except in intercellular channels subtending the stomata.

It should be emphasized in conclusion that a preliminary investigation of the cuticle, epidermis, stomatal apparatuses, and subepidermal layers of the most primitive surviving representatives of the Cactaceae reveal salient trends of structural specialization whose functional significance can be fully and reliably elucidated only by sustained experimental and other observations on plants growing in their native habitats. Such detailed experimental investigations, in adequate correlation with anatomical and enviromental ones, are at present much needed for a clearer understanding of salient adaptations in the Cactaceae which are essential for survival in arid environments.

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## EXPLANATION OF PLATES

### PLATE I

Figs. 1–4. Epidermal layers of leaves, stained in Haidenhein's haematoxylin and sudan III and mounted in glycerin, × 200. 1, *Pereskia grandifolia* [*Castellanos*], epidermal layer from leaf preserved in F.A.A. 2, *Pereskiopsis scandens* [N.Y. Bot. Gard.], epidermal layer from leaf preserved in F.A.A. 3, *Pereskia pititache* [*Boke*], epidermal peel from small thin leaf of young elongating shoot of a greenhouse plant. 4, *Pereskiopsis* [*Boke* B–20], epidermal layer from leaf preserved in F.A.A.

### PLATE II

Figs. 5–9. Cuticular striations and stomatal apparatuses. 5, *Pereskia sacharosa* [N.Y. Bot. Gard.], epidermal peel from leaf stained in sudan III showing radially and irregularly oriented cuticular striations, × 420. 6, *Pereskia pititache* [*Boke*], epidermal layer from large thick leaf of an old tree growing in the wild, stained in sudan III, showing convoluted forms of cuticular striations, × 330. 7, *Pereskia sacharosa* [N.Y. Bot. Gard.], anticlinal section of leaf stained in safranin and haematoxylin, showing stomatal apparatus and subtending intercellular cavity in the chlorenchymatous tissue, × 420. 8, *Pereskia grandifolia* [*Boke*], epidermal peel from leaf, stained in sudan III, showing chloroplasts in guard cells of stomata, × 510. 9, *Pereskia* aff. *humboldtii* [*Ferreyra*], epidermal layer from stem stained in sudan III, showing collapsed guard cells plugged with cutin, × 420.

### PLATE III

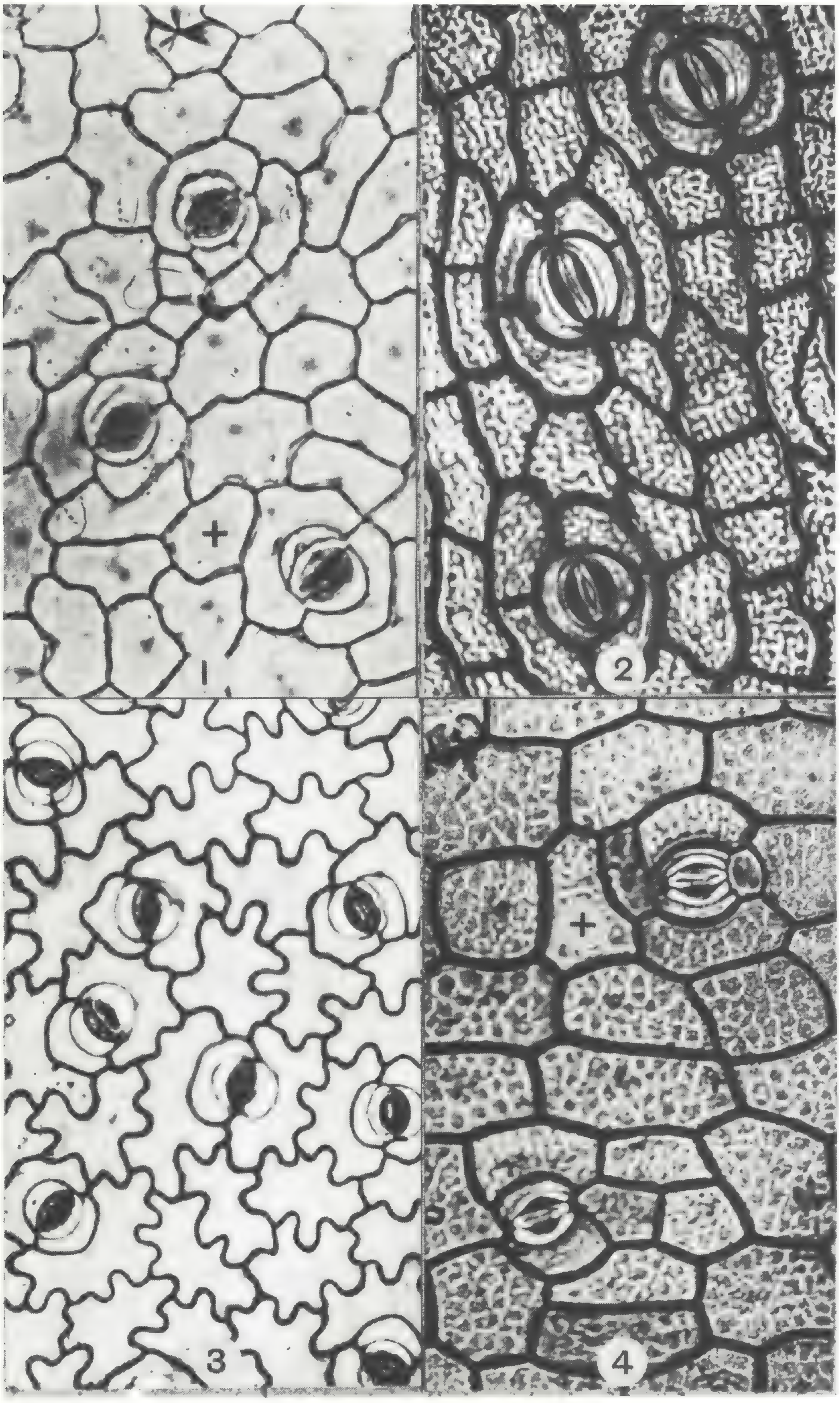
Figs. 11–13. Epidermal layers of stems preserved in F.A.A., stained in sudan III and mounted in glycerin, × 260. 11, *Pereskia grandifolia* [*Castellanos*]. 12, *Pereskia* aff. *bleo* [*Rodriguez*]. 13, *Pereskiopsis scandens* [N.Y. Bot. Gard.].

## PLATE IV

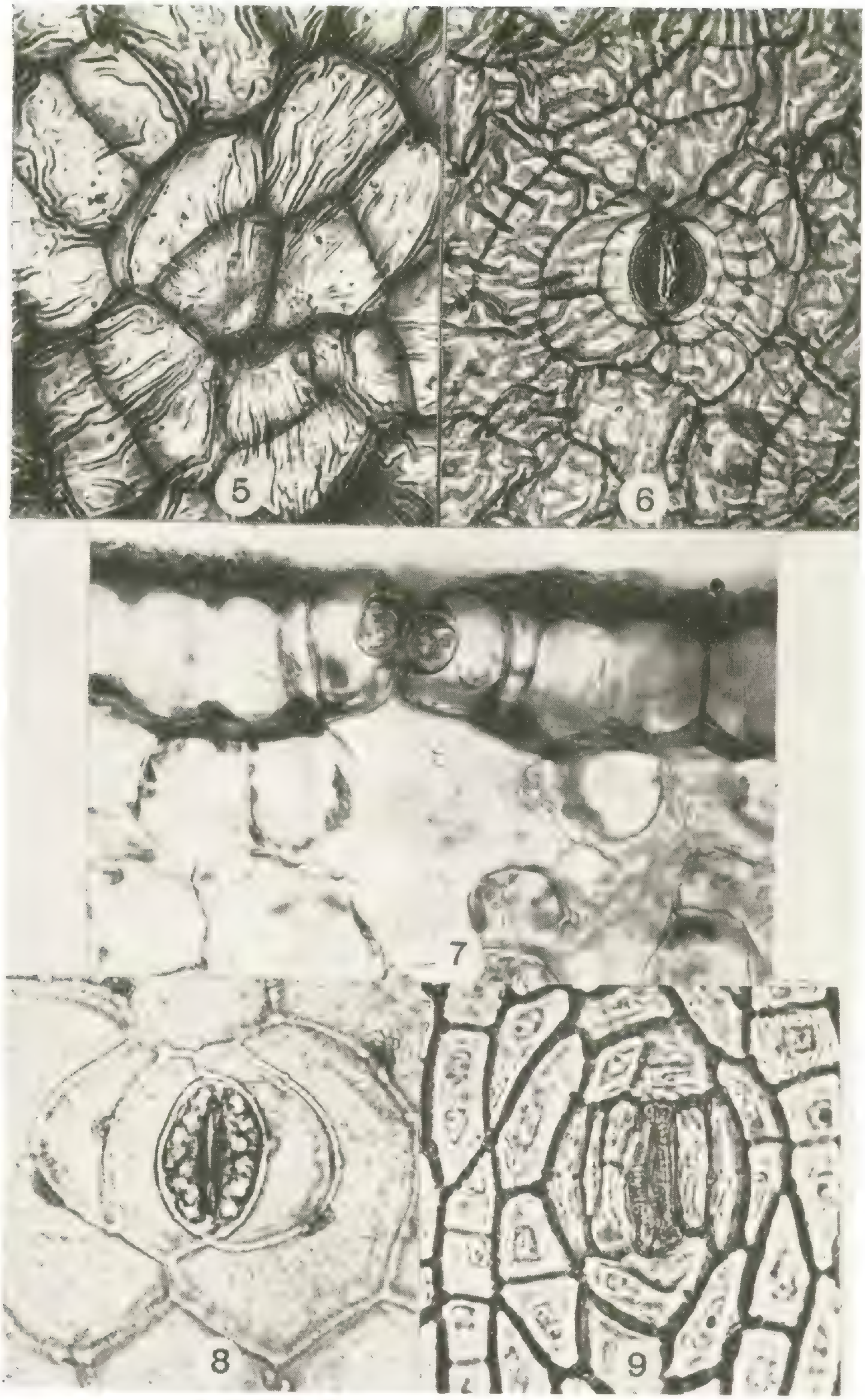
FIGS. 14–18. Sectional views of young stems prior to periderm formation. 14, *Pereskia tampicana* [*Boke*], stained in haematoxylin and safranin, showing cuticle, epidermis, and thin walled cells of mesophyll, × 200. 15, *Pereskia diaz-romeroana* [*Cárdenas*], stained in haematoxylin and safranin, showing cuticular ledges in frontal cavity or vestibule of stomatal apparatus, outer pseudo-collenchymatous layers of cortex appearing black, × 420. 16, *Pereskia grandifolia* [*Moran 7270*], cuticle stained intensely with sudan III and mounted in glycerin, × 420. 17, *Pereskiopsis aquosa* [N.Y. Bot. Gard.], cuticle stained with sudan III, showing massive accumulation of cutin in frontal cavity, overlying the guard cells and penetrating between the guard cells and the subsidiary cells, × 420. 18, *Pereskiopsis porteri* [N.Y. Bot. Gard.], cuticle stained with sudan III showing massive intercellular intrusions of cutin, depression of guard cells inwardly, and marked reduction in their diameter, × 420.

## PLATE V

FIGS. 19–22. Details of collenchymatous and crystalliferous layers. 19, *Pereskiopsis scandens* [N.Y. Bot. Gard.], section of young stem stained in haematoxylin and safranin showing contrast in thickness of walls of the inner chlorenchymatous cortex and the outer collenchymatous layers which are devoid of intercellular spaces except in channels subtending the stomata, × 200. 20, *Pereskiopsis aquosa* [N.Y. Bot. Gard.], showing form of druse in crystalliferous hypodermis, × 510. 21, *The same*, showing form of druses in chlorenchymatous cortex, × 510. 22, *Pereskiopsis chapistle* [Mo. Bot. Gard.], tangential section of collenchymatous layers stained in haematoxylin, showing intercellular channel and character of primary wall "pitting," × 200.




BAILEY, LEAF-BEARING CACTACEAE, XII

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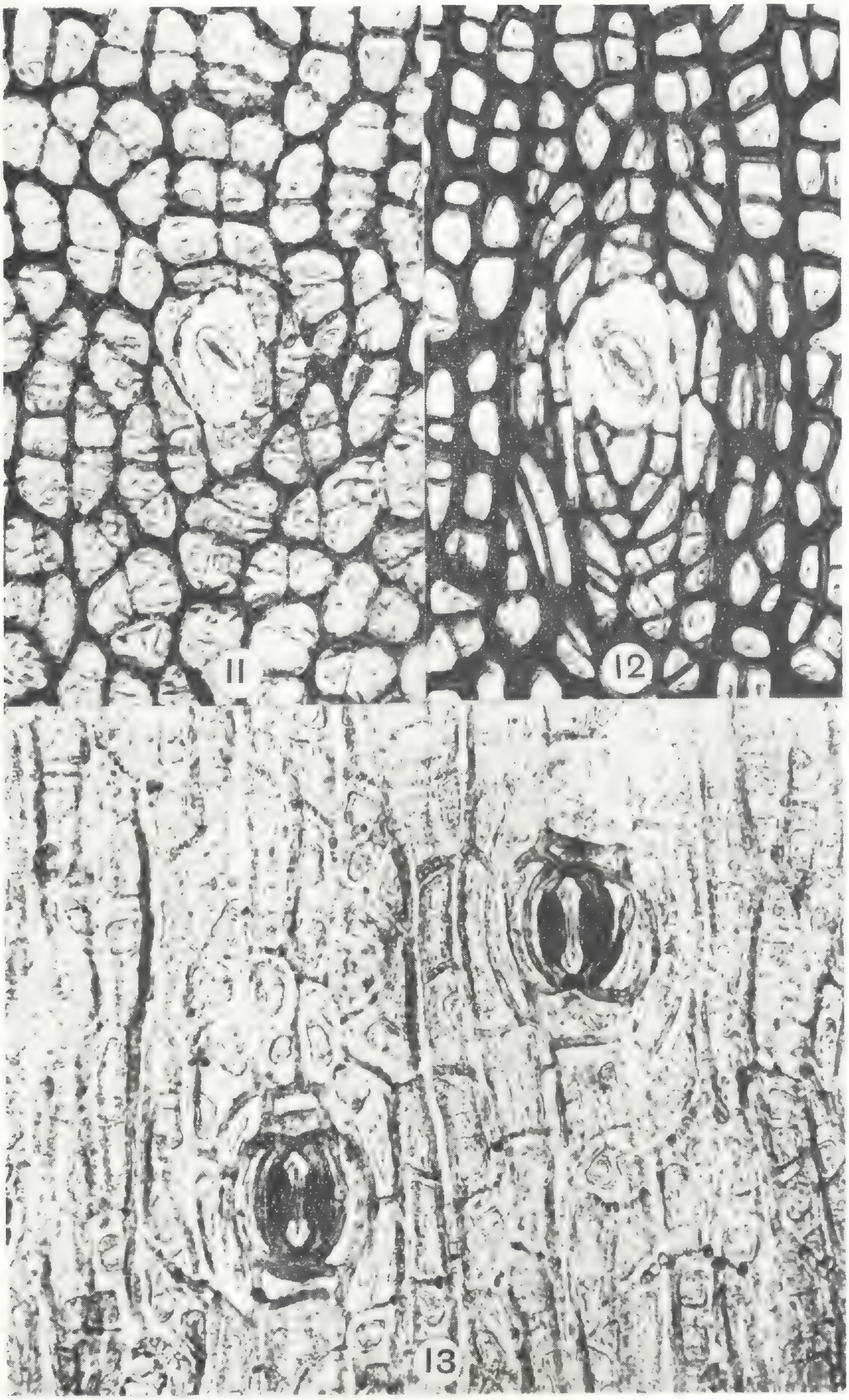


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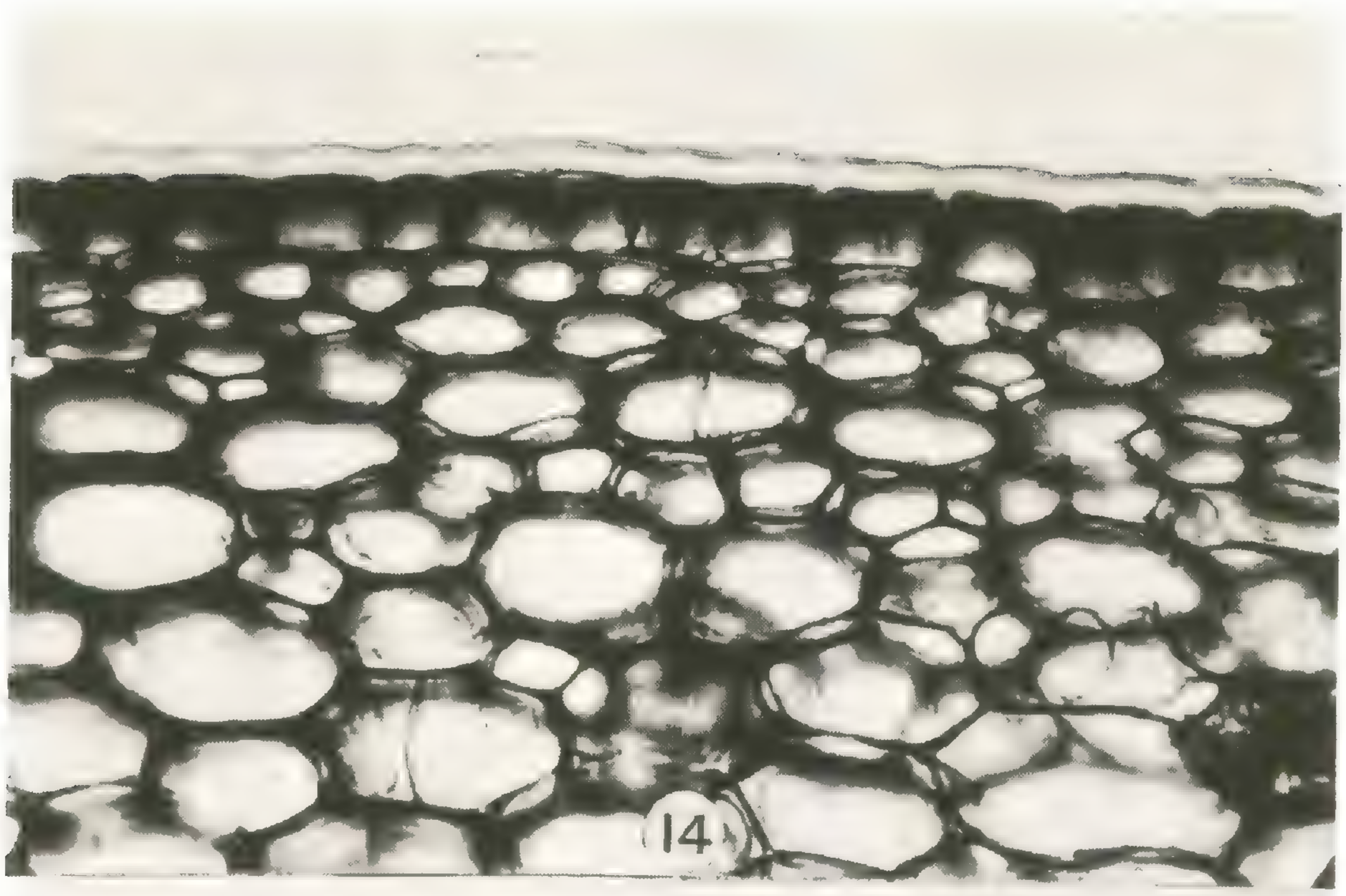
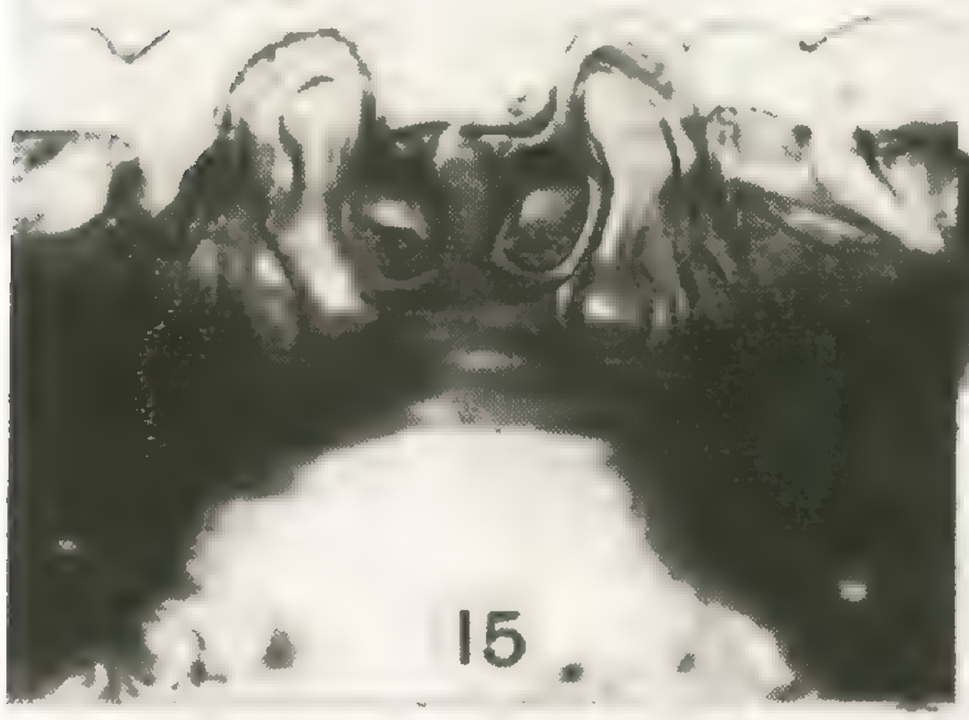
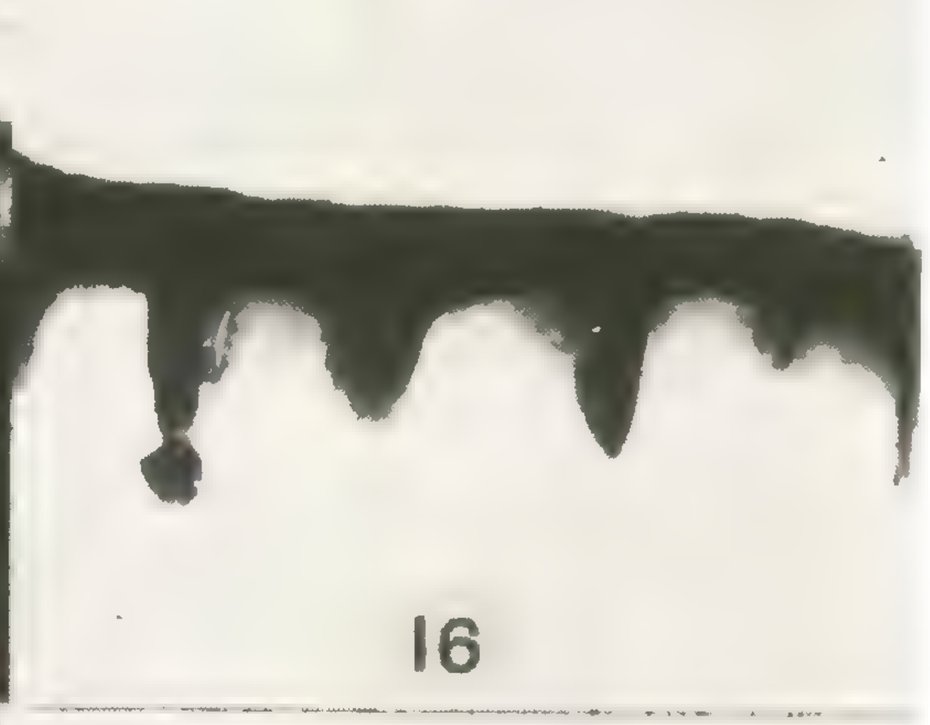
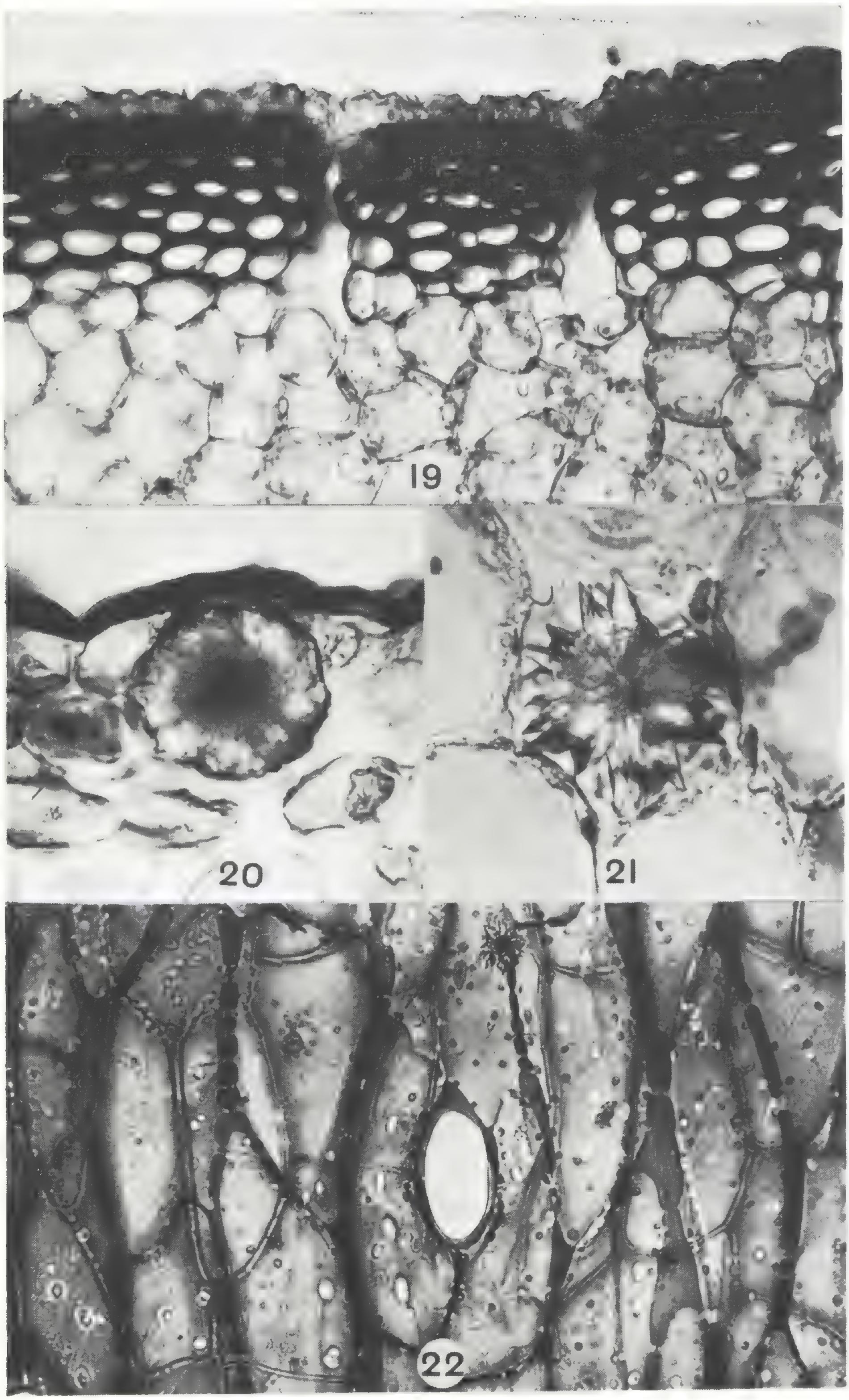


BAILEY, LEAF-BEARING CACTACEAE, XII




BAILEY, LEAF-BEARING CACTACEAE, XII

# SYNOPSIS OF THE GENUS AURINIA IN TURKEY

T. R. DUDLEY [1]

THE GENUS AURINIA Desv. has long been considered a section of *Alyssum* L., but, although both taxa are in the Cruciferae tribe Alysseae, affinity between them appears to be tenuous and remote. The major objection to keeping *Aurinia* as a section of *Alyssum* is that, although composed of a relatively homogeneous group of species, *Aurinia* is anomalous in comparison with the natural sections (i.e., MENIOCUS (Desv.) Hook., PSILONEMA (Meyer) Hook., ALYSSUM, GAMOSEPALUM (Hausskn.) Dudl., TETRADENIA (Spach) Dudl., and ODONTARRHENA (Meyer) Koch) of *Alyssum*. Lines of probable affinity may be traced between these sections, but *Aurinia* does not appear to have any such clearcut relationships. Among the genera of the Alysseae, *Aurinia* seems to be most closely allied to *Berteroa* DC., or possibly to *Alyssoides* Mill.

No taxon presently considered an *Alyssum* possesses the combination of characters which are evident in *Aurinia* and which permit it to be easily recognized, and distinguished feasibly from *Alyssum*. These characters are contrasted in the following table.

| | AURINIA | ALYSSUM |
|---|---|---|
| ROSETTE LEAVES | Usually repand-sinuate, dentate, or pinnatifid, (20–)40–60(–100) mm. long; petioles deeply grooved with swollen bases which are persistent on caudices. | Usually entire; (2–)5–15(–20) mm. long; petioles flat and attenuate, bases never swollen or persistent on caudices. |
| CAULINE LEAVES | Reduced, 1/2 (or less) the size of the rosette leaves. | More or less equal in size to the rosette leaves. |
| FERTILE STEMS | Sparsely foliate, often nearly scapose. | Always leafy, never scapose. |
| FLOWER BUDS | Globose, as long as broad. | Elliptic and oblong. |
| CALYX | Cup-shaped, with sepals widely spreading at maturity. | Elongate, with sepals erect at maturity. |
| STIGMAS | (Immature) conspicuously bilobed. | Globose, rarely bilobed. |

[1] The assistance of Dr. James Cullen, Department of Botany, University of Edinburgh, Scotland, is gratefully acknowledged, as well as that extended by Dr. Bernice G. Schubert of the Arnold Arboretum.

**Aurinia** Desv. Jour. Bot. 3: 162. 1814 (!). LECTOTYPE SPECIES: *Alyssum saxatile* L. Sp. Pl. 2: 650. 1753 (= *Aurinia saxatilis* (L.) Desv. *loc. cit.*). — Meyer in Ledeb. Fl. Ross. 1: 136. 1842. — Griseb. Spic. Fl. Rum. & Bith. 1: 271. 1843. — Koch, Hort. Dendrol. 23. 1853. — Schur, Enum. Pl. Transsilv. 61. 1866.

*Alyssum* sect. *Anodontea* DC. Syst. Nat. 2: 317. 1821 (!). LECTOTYPE SPECIES: *Alyssum edentulum* Waldst. & Kit. (= *Aurinia petraea* (Ard.) Schur).

*Anodontea* (DC.) G. Don, Gen. Hist. Dichl. Pl. 1: 180. 1831 (!).

*Anodontea* sect. *Vesicaria* sensu G. Don, loc. cit. (!), non *Vesicaria* Adans.

*Alyssum* sect. *Aurinia* (Desv.) Koch, Syn. Fl. Germ. & Helv. 1: 58. 1837 (!). — Boiss. Fl. Or. 1: 263 & 265. 1867. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. 17b: 491. 1936. — Busch in Komarov, Fl. U.R.S.S. 8: 348. 1939. — Nyár. Anal. Acad. Rep. Pop. Rom. Secţ. Ştiinţe Geol. Geog. Biol. ser. A. mem. 3. 1: 8. 1949.

*Aurinia* sect. *Corioceratium* Griseb. Spic. Fl. Rum. & Bith. 1: 272. 1843 (!). LECTOTYPE SPECIES: *Aurinia saxatilis* (L.) Desv.

*Lepidotrichum* Velen. & Bornm. Oesterr. Bot. Zeitschr. 39: 324. 1889 (!). TYPE SPECIES: *Lepidotrichum uechtritzianum* (Bornm.) Velen. & Bornm.

*Plants* perennial, or biennial. *Rosette leaves* up to 100 mm. long, with repand or sinuate or dentate to pinnatifid margins and deeply grooved petioles with swollen and persistent bases (except *Au. halimifolia*), usually distinctly rosulate and conferted on indurated caudices. *Cauline leaves* reduced, usually ½ (or less) the size of rosette leaves. *Fertile stems* sparsely foliate, often nearly scapose. *Indumentum* of stellate or lepidote hairs with few or many branched or unbranched rays. *Inflorescence* unbranched and racemose, or multibranched, corymbose or paniculate. *Pedicels* divergent and spreading. *Flower buds* globose, as long as broad. *Calyx* cup-shaped. *Sepals* 4, widely spreading at maturity, free, never truly saccate. *Petals* 4, yellow or white, bifid or entire, spathulate and clawed. *Long filaments* 4, always free, equally bilaterally winged and dilated at bases, often with small basal teeth. *Short filaments* 2, winged with small basal teeth. *Anthers* short, obtuse, filament tips never prolonged. *Nectaries* 4, globose or triangular, one at each side of short filaments. *Styles* of varying lengths, often widely dilated to bases, persistent. *Stigmas* (immature) conspicuously bilobed. *Silicles* latiseptate, always dehiscent, glabrous or rarely with indumentum (only *Au. rupestris*), bilocular with conspicuous repla, locules 2–4(–6)-ovulate with placentation nearly apical, or rarely lateral (*Au. halimifolia* & *Au. leucadaea*); valves compressed or subinflated, or equally inflated and turgid. *Seeds* winged, or rarely wingless (*Au. uechtritziana*), not mucilaginous. *Embryo* notorrhizal.

DISTRIBUTION: Central and southern Europe, east to the Ukraine and the Caucasus, north to Poland, and in Turkey.

SPECIES NOT OCCURRING IN TURKEY:

*Au. corymbosa* Griseb. Spic. Fl. Rum. & Bith. 1: 271. 1843 (!). The Balkans.

*Au. halimifolia* (Boiss.) Cullen & Dudley, comb. nov.[2] The maritime Alps of France and Italy.

*Au. leucadaea* (Guss.) Koch. Hort. Dendrol. 23. 1853 (!). Yugoslavia and Italy.

*Au. petraea* (Ard.) Schur, Enum. Pl. Transsilv. 61. 1866 (!); Fuss, Fl. Transsilv. 64. 1866, possibly the earlier combination, fide *Index Kewensis*. Central and southeastern Europe. Escaped from cultivation in New York State.

## KEY TO SPECIES OF AURINIA OCCURRING IN TURKEY

A. Inflorescence compound, multibranched, corymbose; margins of rosette leaves always repand or sinuate, or dentate to pinnatifid; indumentum of stellate hairs, few or many rayed, never lepidote; valves of silicles membranous and smooth.
  B. Flowers yellow; seeds broadly winged; silicles (3–)4–8(–12) × (2–)3–8(–15) mm., valves compressed or only slightly inflated at center; inflorescence 5–15(–20) cm. long; fertile stems greenish, with sparse indumentum. ..... 1. *Au. saxatilis*.
  B. Flowers white; seeds wingless; silicles 2–4 × 2–2.5 mm., valves turgid, strongly and equally inflated; inflorescence 20–40 cm. long; fertile stems whitish with dense indumentum, especially towards base. ..... 2. *Au. uechtritziana*.

A. Inflorescence simple, unbranched, racemose; margins of rosette leaves always entire; indumentum of strongly lepidote hairs; valves of silicles cartilaginous and prominently ridged at apex. .. 3. *Au. rupestris*.

1. **Aurinia saxatilis** (L.) Desv. Jour. Bot. 3: 162. 1814 (!). — Kotov, Fl. Ukraine **5**: 329. *pl. 75*. 1953.

1. Silicles elliptic or obovate, 3–5(–6) × 2–4(–5) mm., always longer than broad, obtuse or acute, rarely emarginate; styles 0.5–1 mm. long, not conspicuously dilated to bases; margins of rosette leaves sinuate, or only sparsely dentate, with teeth not more than 0.5 mm. long. a. Subsp. *saxatilis*.
1. Silicles orbicular or oblate, 3.5–10(–12) × 4–12(–15) mm., usually wider than long, emarginate or truncate (or if obtuse or acute, then silicles 8–10(–15) mm. long and wide, and styles 2–5.5 mm. long); styles 2.5 mm. long, strongly dilated at bases (bases 0.5–0.8 mm. in diameter; apices 0.1–0.2

[2] **Aurinia halimifolia** (Boiss.) Cullen & Dudley, comb. nov. *Ptilotrichum halimifolium* Boiss. Voy. Bot. Mid. Esp. **1**: 45. 1839, non *Alyssum halimifolium* Willd. Linn. Sp. Pl. ed. 4. 3(1): 460. 1800, nomen illeg. nec *Alyssum halimifolium* L. Sp. Pl. *2*: 650. 1753 ( = *Lobularia maritima* (L.) Desv.). Boissier's combination is treated as a new name (cf. note to Article 72, *Internat. Code of Bot. Nomencl.* 52. 1961). Accordingly, the basionym of *Aurinia halimifolia* is *Ptilotrichum halimifolium* Boiss., not *Alyssum halimifolium* Willd.

mm. in diameter); margins of rosette leaves strongly dentate, often pinnatifid, with teeth (0.5–)1–5 mm. long (or if margins entire, then plants very reduced, only 5–10 cm. tall).

2. Silicles 3.5–6 mm. × 4–7 mm.; pedicels 4–10 mm. long; styles 1–1.5 mm. long; petals 3–4(–4.5) × 1.5–2 mm.; wings of seeds 0.4–0.5 mm. wide. ..... b. Subsp. *orientalis*.
2. Silicles 6–12 × 8–15 mm.; pedicels (7–)10–20 mm. long; styles (1.5–)2–2.5 mm. long; petals (4.5–)6–7 × (2–)2.5–3.5 mm.; wings of seeds (0.5–)0.7–1 mm. wide. ..... c. Subsp. *megalocarpa*.

Subsp. **saxatilis**

*Alyssum saxatile* L. Sp. Pl. **2:** 650. 1753 (!). Holotype, cultivated in the Leiden Botanic Garden (L, hb. *Royen*; hb. lugdb. Bat. no. 901050). — Reichenb. Ic. Bot. **3:** 30. *t. 232.* 1825; Ic. Fl. Germ. & Helv. **2:** 9. *t. 21, fig. 4280.* 1837–1838. — Mansfeld, Repert. Sp. Nov. **46:** 115. 1939. — Nyár. Fl. Rep. Pop. Rom. **3:** 327. *pl. 56, fig. 2.* 1955. — Moravec, Preslia **32:** 360. 1960.

*Alyssum arduinii* Fritsch, Exc. Fl. Öst. 253 & 268. 1897 (!); in Kerner, Sched. Fl. Aust.-Hung. **9:** 24. 1902.

*Alyssum arduinii* subvar. *lamprocarpum* Borb. Balaton Fl. 391. 1900. Holotype, Hungary. Túl-a-Dunán, *Borbás* (BP, non vidi). — Jáv. & Csap. Ic. Hung. **7:** *pl. 213, figs. 1600 & 1600a.* 1930.

*Alyssum saxatile* var. *typicum* Beck, Glasn. Zem. Muz. Bosn. Herceg. **28:** 129. 1916 (!).

*Alyssum saxatile* var. *arduinii* (Fritsch) Hayek, Prod. Fl. Pen. Balc. **1:** 430. 1925 (!).

*Alyssum saxatile* subsp. *arduinii* (Fritsch) Paw. Fl. Tatrorum. **1:** 325. 1956 (!).

DISTRIBUTION AND HABITAT: Widespread on calcareous substrates in central and southeastern Europe, extending east to the Ukraine and the upper Caucasus, and north into Poland, alt. up to 1000 m. Fl. Apr.–June.

**Europe.** FRANCE: Bei Muggendorf, fränk. Jura, 410 m., *Reinsch 157* (E, GH, K, W). GERMANY: 1889, *Dresler* (GH); Muggendorf, 1838, *Souder* (E); Aug. 1840, *Koch* (K); *Koch 11 bis* (BM, GH, K, W). AUSTRIA: ad Danube, *Kerner* (K, W); Wien, *Kerner* (GH, K, W); ad Danubium pr. Melk, *Strobl* (BM, E, G, GH, K, W); pr. Krems (E); Thaya bei Zaabs, May–June 1871, *Krenberger* (BM, GH, K, W). CZECHOSLOVAKIA: Thajortal, *Obrony 160b* (BM, E, G, GH, K, W); Burberg bei Kaaden, *Stelzharmer 760* (BM, E, G, GH, K, W); Moravia, Rosenstein ad Mikulov (Nikolsburg), 450 m., *Sirjaev 219* (BM, GH, K, W); Znaim, *Oborny* (BM, E, G, GH, K, W); Valle Radstinské, urb. Praha, May 1938, *Milaš* (BM, E, K, GH, W); Bohemia, *Stekhemak 160* (E, W). HUNGARY: Buda, May–June 1876, *Richter* (E, W); Budors pr. Ofen, *Richter 11* (BM, GH, K, W); Esckerberg, *Tauscher s.n.* (E, W); Mt. St. Gerade, *Schiffer* (E, W); Comit. Zala, mont. Szent-Gyorgyhegy ad Kisapati, 250 m., *Kümmerle 189* (BM, E, G, GH, K, W); Comit. Pest., mont. Töröku-grato, pr. Budaörs, 200 m., 6 June 1913, *Jávorka* (BM, GH, K, W); Buda, *Ball* (E, GH). YUGOSLAVIA: Macedonia, Sor. Planina, Popova Sapka, 30 miles west of Skopje, 210 m., *Stainton 7962* (K, W); Serbia Suva Planina, pr. Babuschnitza, *Rechinger 16036* (W); Djep, *Ilić* (E, W). BULGARIA:

*Noë 4280* (E, K); Rhodope hills, *Turrill ?* (BM, K). ROMANIA: Matschan, Dobrudscha, 1873, *Sintenis 576* (G, K, W); Guravoie, 15 July 1895, *Degen* (BM, E, K, G, W); Transsilvania, Koppandi-Hasadek, pr. Torda, *Wolff* (BM, E, G, GH, K, W). RUSSIA: Konuva, 28 Mar. 1903 (E); Borythreum (Borysthenis), July 1820, *Steven* (BM, G-DC); Podolia, 1820, *Andrzejowski* (G-DC).

Fritsch, in Kerner (1902), who pointed out that Linnaeus (*Species Plantarum*, 1753) cited polynomials from Royen, and from Tournefort for *Alyssum saxatile* (the basionym of *Aurinia saxatilis*), correctly maintains that the polynomial from Tournefort, *Corollarium Institutionum*, 15. 1703, which reads: "Alyssum creticum saxatile, foliis undulatis incanis" is synonymous with *Alyssum orientale* Ard. (subsp. *orientalis* (Ard.) Dudl.). Furthermore, because of Linnaeus's discordant references, Fritsch applied a *nomen novum*, *Alyssum arduinii*, to refer to that part of *Alyssum saxatile* which was based on the polynomial from Royen, *Florae Leydensis*, 33. (1740) reading: "Alyssum caulibus frutescentibus paniculatis, foliis lanceolatis undulatis integris." Examination of Royen's original specimen in the Leiden herbarium proves without any doubt that it is subsp. *saxatilis*, and not subsp. *orientalis*.

The three well developed subspecies which are recognized in *Aurinia saxatilis*, subspecies *saxatilis*, *orientalis*, and *megalocarpa*, are morphologically distinct, and have characteristic distributions. Subspecies *saxatilis*, the northern and most widespread in the species, is almost entirely replaced in the Balkans and Aegean region by subsp. *orientalis*. Whereas subsp. *orientalis* is only partially sympatric in the northern Balkans with subsp. *saxatilis*, subsp. *megalocarpa* is completely sympatric, in terms of geography, with subsp. *orientalis*.

Subsp. **orientalis** (Ard.) Dudley, comb. nov.

*Alyssum orientale* Ard. Animad. Bot. Spec. Alt. 2: 32. *t. 15, fig. 1.* 1764 (!). Type, "ab Oriente," *Arduino* (PAD, non vidi).[3] — Boiss. Fl. Or. 1: 266. 1867. — Velen. Fl. Bulg. 37. 1891.

*Clypeola tomentosa* L. Mantissa, 92. 1767 (!). Holotype, "ab Oriente," *Arduino* (LINN no. 828:3).

*Alyssum affine* Ten. Syll. Fl. Neap. 315. 1831 (!). Holotype, Italy. In saxosis Japygiae: Lecce, Martina, 1819, *Tenore 23716* (NAP, non vidi); isotypes (G-DC; K, no. 303 sent in 1824, and one sheet ex herb. Gay; GH, sent in 1846).

[3] Seeds from the Orient, which were given to Arduino by Dr. Leonardo Seslerio were grown in the Padova Botanic Garden. Arduino states that the original description and figure of *Alyssum orientale* were based on two cultivated specimens in his herbarium, grown from these seeds. Evidently there were more than two specimens originally, because in 1761 Arduino sent a specimen to Linnaeus. This specimen no. 828:3 in the Linnaean herbarium (LINN) was annotated by Linnaeus "Ard.", indicating the source of the specimen. This Arduino duplicate, and the description and figure of *Alyssum orientale*, served as the basis of *Clypeola tomentosa* L. (1767), a synonym of *Alyssum orientale*, and accordingly of *Aurinia saxatilis* subsp. *orientalis*. There may be additional specimens, cultivated from the seeds given to Arduino by Seslerio, in the herbaria of the Botanical Museum in Copenhagen and the University of Firenze.

[b]*Aurinia orientalis* (Ard.) Griseb. Spic. Fl. Rum. & Bith. **1:** 272. 1843 (!).
*Alyssum orientale* var. *majus* Hausskn. Mitt. Thür. Bot. Ver. **3–4:** 112. 1893 (!). Holotype, Greece. In decliv. nemorosis infra Mon. Korona, Pindus Dolopicus, 1067–1097 m., 20–28 June 1885, *Heldreich* (JE, non vidi); isotypes (BM, E, G, K).
*Alyssum saxatile* var. *alpinum* Hal. Denkschr. Akad. Wien Math. Naturw. **61:** 496. 1894 (!). Holotype, Greece. In der oberen Region der Kyllene oberhalb Gura, *Halácsy* (W).
*Alyssum denticulatum* Form. Verh. Natur. Ver. Brünn **32:** 177. 1894. Holotype, Yugoslavia. In saxosis ad urbem Ochrida in Macedonia, *Formánek* (BRNU, non vidi). — Vandas, Reliq. Formánek. 35. 1909.
*Alyssum saxatile* var. *majus* (Hausskn.) Hal. Consp. Fl. Gr. **1:** 91. 1900 (!).
*Alyssum saxatile* var. *albidum* Tuzs. Bot. Kozlem. **8:** 266. 1909 (!). Lectotype, Crete. Cap. Maleca, *Sieber* (BM, E, GH, K, W).
*Alyssum saxatile* var. *orientale* (Ard.) Beck, Glasn. Zem. Muz. Bosn. Herceg. **28:** 129. 1916 (!). — Hayek, Prod. Fl. Pen. Balc. **1:** 430. 1925.
*Alyssum saxatile* var. *orientale* f. *maius* (Hausskn.) Hayek, *loc. cit.* (!).
*Alyssum saxatile* subsp. *orientale* (Ard.) Rech. f. Ann. Naturh. Mus. Wien **43:** 300. 1929 (!).
*Alyssum orientale* f. *humilis* Vierh. Oesterr. Bot. Zeitschr. **84:** 138. 1935 (!). Holotype, Crete. Hagios Vasilis, alpine Stufe des Kedros, 19 Apr. 1904, *Dörfler 561* (WU); isotypes (BM, G, K).
*Alyssum saxatile* auct. Levanticum — Sibth. & Smith, Ic. Fl. Gr. **7:** 21. *t. 624.* 1830. — Hal. Consp. Fl. Gr. **1:** 90. 1900. — Bornm. Mitt. Thür. Bot. Ver. **24:** 11. *fig. 2.* 1909.

DISTRIBUTION AND HABITAT: Saxatile on calcareous substrates in Calabria in southern Italy, the Balkans, the Aegean Islands, Crete, Turkey-in-Europe, and the western coast of Anatolia; alt. 50–1500 (–2286) m. Fl. Apr.–May.

ITALY: Calabria, Catanzaro, near Tiriolo, *Rigo 312* (A, K, W); Mt. Tiriolo, near Castrovillari & Mt. Pollina, 400–800 m., *Huter, Porta & Rigo 235* (BM, E, K, W); San Pietro in Devafane, May 1874, *Groves* (BM, K); near Rossano, *Lacaita 104/24* (BM); 1820, *Dierville* (G-DC). Italia meridionalem, 1819, *Moratti* (G-DC). YUGOSLAVIA: Macedonia, Ohrid, *Rechinger 15927* (K, W); 20 miles south of Skopje, Katlanova, 305 m., *Stainton 7819* (K). ALBANIA: Bertiscus, Pecska Bistrica near Peč (Ipek), 600–750 m., *Rechinger & Scheffer 124* (K, W); Sant. Graminta, 1897, *Baldacci* (BM). CORFU: San Deca, 7 May 1878, *Spreitzenhofer* (GH, K); pass to Paleocastuzza, Apr. 1855 (K); H.T. (K); ex hb. Montbret (W); pass. Panteleimon in Skripero, 126–317 m., 10 May 1896, *Baenitz* (E, K, W). BULGARIA: Montes Stara Planina, fluv. Isker near Lakatnik, *Rechinger 1741* (W); in sax. ad Sveti Dimitri near Basarbova, *Rechinger 569* (W); Dermende, May 1890, *Pichler* (G, W); Kricin, May 1895, *Střibrný* (E, K, W); May 1902, *Střibrný* (E, K, W); Kritchma, 27 June 1896, *Střibrný* (E, K, W); Tekir, 9 June 1895, *Střibrný* (E, K, W); Eli Dere, May 1907, *Střibrný* (E, K, W). ROMANIA: Kleine Karpathen, Ruine Tallenschein bei Theben-Neudorf, June 1902, *Schneider* (A, W); Danubii, inter Verciorova et Guravoie, et inter Svintza et Drenkova, *Degen 3268* (BM, E, GH, K, W). CRETE: *Tournefort* (BM); Kissamos, Polyrrhenen, *Gandoger 8736* (BM, K); Cap Makea, Canée, *Gandoger 82101* (BM, K). GREECE: *Sibthorp 1057* (OXF); Attica, Mt. Parnes, Ilatoci,

500 m., *Samuelsson & Zander 120 & 476* (E, GH, K); 1000 m., *Rechinger 585b* (W); *Heldreich 2693* (G, W); Athens–Phaleron, *Patten 196* (GH); Acropolis, Athens, 23 Mar. 1900, *Patten D* (GH); *Spruner* (G, GH, K, W); Mar. 1876, *Pichler* (G, GH, K, W); 1889, *Sintenis 15* (W); Feb. 1847, *Heldreich* (E, W); 1843–1844, *Heldreich* (E); *Heldreich 412* (BM, K); Athens, Lycabetho, Mar. 1862, *Heldreich* (G, GH, K); 60–457 m., *Orphanidis 276* (BM, E, G, GH, K, W); *Schrenk 27* (W); *Davis 93* (BM, E); *Heldreich 1112* (K); Mar. 1842, *Boissier* (G, GH, K, W); Ardetto near Athens, *Heldreich 1112b* (BM, K); Thena ad Acropolis, Oct. 1867, *Ball* (E); Hieropolis, *Spruner* (K); Attica, *Guiol 915* (BM); Mt. Hymetto, Mar.–Apr. 1847, *Heldreich* (E, W); Chelmos, 228 m., *Davis 990* (E); *Lemperg 1088* (K); Phocis near Delphi, *Leonis 383* (A, E, G); Turkovinis near Athens, 7 Apr. 1927, *Rechinger* (W); Kymelti versus Tankrati, *Rechinger 482* (W); near Kalanistra, 500 m., 11 June 1893, *Halácsy* (W); Thessalia, Agris prope Volo [Vólos] (Tersana), 1896, *Sintenis 70 & 71* (BM, GH, K, W); Volos, *Rechinger 22609* (W); Makiniata near Volo, *Polunin 6552* (K); in valle Tempe fluv. Peneios, prope Rapsani, *Rechinger 22572* (W); Kasabaliotiko pr. Kasabali, *Rechinger 1190* (W); Kastri pr. lacus Karla, *Rechinger 22842* (W); Pelion pr. Volos, 800–1500 m., *Rechinger 22718* (W); Macedonia, Gjefgjeli, *Rechinger 1525* (W); fluv. Angista pr. Phorolivos opp. Drama, *Rechinger 6171* (K, W); Salonika, Lembert hills, 1 May 1917, *Wilson* (E); Epirus, dist. Zagorion, fluv. Voidomatis, 17 km. versus Joannina, *Rechinger 21428* (W); Mt. Tymphi, fluv. Vikos, 300–800 m., *Rechinger 21149* (W); inter Vriskos et Joannina, *Rechinger 20719* (W); pr. Klissoura, 47 km. south of Joannina, 400 m., *Rechinger 23327* (W); 20 km. south of Joannina, *Rechinger 23263* (W); Euboea, *Aucher 239* (BM, K, OXF); pr. Steni, 350–500 m., *Rechinger 1921* (K, W); in montis Xiron Oros pr. Hagia Anna, 750–950 m., *Rechinger 17111* (W); Psachna et Achmet Aga (Prokopion) a Hagios, 300–500 m., *Rechinger 16500* (K, W); Mt. Kandili, 10 km. ab Achmet Aga, 300 m., *Rechinger 18166* (W); a Limni, *Rechinger 16686* (W); Thrace, Derbend, 10 km. north of Alexandriopolis, *Rechinger 22258* (W); Lignitorichion et Potamos pr. Alexandriopolis, *Rechinger 6048* (K, W); north of Arvas, 200 m., *Ball 522* (LIVU); Mt. Karlik-Dagh pr. Komotini (Gumuldschina), 1400 m., *Rechinger 10497* (K, W); fluv. Nestos (Mesta), pr. Toxotai (Oktschilar), 60–100 m., *Rechinger 9649, 9349, 9812* (W); *Rechinger 10497, 10966* (W); Montes Rhodope supra pr. Iasmos (Jasi-Koj) *Rechinger 9525* (W); Mesta valley, *Tedd 547* (K); above Yassikeuy, 366 m., *Tedd 1805* (K); Mt. Xanthi, 120 m., *Tedd 2196* (K); near Heraclitera, 90 m., *Tedd 1964* (K); Kizil Ada, 762 m., *Tedd 1956* (K); Peloponnesus, Laconia, Pen. Mani, supra Porto Kalion, *Rechinger 20134* (W); Korinthia, lacum Stymphalia, *Rechinger 10534* (W); Akropkari, *Rechinger 573* (W); Messenia, Verga ad Kalamai (Kalamata) ad Mt. Taygetos, *Rechinger 20400* (W); 950 m., *Bornmüller 119* (W). AEGEAN ISLANDS: Samothrake, Mt. Phengari, 500–1400 m., *Rechinger 9812* (K, W); 28 June 1934, *Tedd* (K); Thasos, Mt. Isparion, 1097 m., *Tedd 1886* (K); Sporadum, Kyria Panagia, Reiser Insel, Hagios Petros, *Rechinger 1045* (K, W); Chios, Kardhámyla, *Platt 420* (K); Haghios Georgios, Sykovaro, *Platt 46* (K). TURKEY: A2 (E); Prov. Istanbul, Bosphorus, near Fanar, *Sibthorp* (OXF); Rumelia, Kartova, 1836, *Frivaldsky* (BM, E, K); B1; Prov. Çanakkale, Giaow Hissar, valley of Rhodius, Apr. 1856, *Kirk* (E); Seidinlii in mont. Arablar-Depressi, 1883, *Sintenis 226* (BM); Prov. Izmir, Smyrna, Sedcheni, 27 Apr. 1870, *Peyronin* (G); Koukoularoudja, *Balansa 62* (BM, E, G, K, W); *Whittall 414* (E); Mt. Sipylo (Manisa dağ), 250 m., 1906, *Bornmüller 9084* (BM, E, G, K, W); C2, Prov. Denizli, Denizli-Acipayam, 25 km. from Denizli, 860 m., *Dudley, D. 35340* (A, E, K).

Specimens intermediate between subsp. *saxatilis* and subsp. *orientalis*. YUGOSLAVIA: Macedonia, lacus Ohrid pr. Pistani, 17 km. a Sveti Naum, *Rechinger 19717* (W); fluv. Radika inter Debar et Mavrovi Hanovi, *Rechinger 15795* (W). BULGARIA: Macedonia, Tartorly, 25 May 1917, *Nixolaff* (GH, W).

Specimens intermediate in morphology between subsp. *saxatilis* and subsp. *orientalis* may be found in the area (primarily in the northern Balkans) where these two subspecies overlap. The occurrence of intermediates and the southern distribution of subsp. *orientalis*, replacing subsp. *saxatilis*, indicate that subspecific rank is the most appropriate. The density of indumentum, the degree of leaf lobation or dentation, and the stature of the plants of subsp. *orientalis* show considerable variation. Often the indumentum is denser, the leaf teeth fewer and less pronounced, and the plants dwarf at altitudes above 1500 meters. This does not, however, appear to be a constant pattern. Recognition of these variations has accounted for the varieties listed in the synonymy.

Subsp. **megalocarpa** (Hausskn.) Dudley, comb. nov.

*Alyssum orientalis* var. *megalocarpum* Hausskn. Mitt. Thür. Bot. Ver. **3–4:** 112. 1893. Holotype, the Aegean island of Chios. Bl: In saxosis ins. Chios. 1853, *Pauli* (JE, non vidi). — Bornm. Engl. Bot. Jahrb. **59:** 449. 1925.

*Alyssum ephesium* Bornm. Mitt. Thür. Bot. Ver. **24:** 11. *fig. 1.* 1909 (!). Holotype, Turkey, C1: Ad Ephesi ad moenia dirupta, 1 June 1906, *Bornmüller 9083* (B, non vidi); isotype (OXF).

*Alyssum saxatile* subsp. *megalocarpum* (Hausskn.) Rech. f. Beih. Bot. Centr. **54**(B): 611. 1936 (!). — Rech. f. Fl. Aegaea, 223. 1943.

DISTRIBUTION AND HABITAT: Saxatile on calcareous substrates in the Cyclades, Sporades, western Aegean Islands, and the western coast of Anatolia; alt. 150–610(–1219) m. Fl. Apr.–May.

GREECE: Peloponnesus, Laconia, Pen. Malea, Monemvasia, *Rechinger 20093* (K, W). AEGEAN ISLANDS: B1, Chios, Scio, 1822, *Oliver* (G-DC); near Vrontados, *Gathorne-Hardy* 474 (E); Tal, valley of Livadi, 500 m., *Rechinger 5311* (E, K, W); Lesbos, Malea near Philia, *Candargy* (*fide* Rech. 1943); C1, Kos, Mt. Dikios Asphendiu near Pyli, *Forsyth-Major 642* (A, BM, GH, K, W); 800 m., *Rechinger 8023* (E, K, W); inter Pili & Kardamena, *Rechinger 7981* (K, W); C1, Samos, Mt. Kakis, 610–1219 m., *Davis 1672* (BM, E, K); Mt. Ambelos, 700 m., *Rechinger 3903* (E, G, K, W); Mt. Kerki, 1200 m., *Rechinger 1966* (E, K, W); 1000 m., *Rechinger 4125* (E, K, W); ad monasterium Zoodochus Rigi, 300 m., *Rechinger 3715* (E, K, W); *Amorgos*, ad Langada, Mt. Krikelas, *Rechinger 2352* (W); *Davis 955* (K); 500 ft., *Davis 1433* (A, BM, E, K). TURKEY: C1, Prov. Aydin, Ruins of Priene, 150 m., *Dudley, D. 34972a* (A, E); 20 miles from Söke, *Davis 25231* (BM, E, K).

Subspecies *megalocarpa* is distinguished from subsp. *orientalis*, with which it is sympatric, entirely by the quantitative characters listed in the key to subspecies. The area of distribution of subsp. *megalocarpa* is relatively limited in comparison to that of subsp. *saxatilis* or subsp. *orientalis*, and is completely contained within the range of subsp. *orientalis*.

There appears to be little morphological intergradation between subsp. *orientalis* and subsp. *megalocarpa*. The fruits of some gatherings of subsp. *orientalis* (determined as *Alyssum affine*), however, from Calabria in Italy (e.g., *Rigo 312*) approach in size some of the smaller fruited specimens of subsp. *megalocarpa* from the Aegean Islands (e.g. *Forsyth-Major 642*).

2. **Aurinia uechtritziana** (Bornm.) Cullen & Dudley, comb. nov.

*Ptilotrichum* (*Koniga*) *uechtritzianum* Bornm. Österr. Bot. Zeitschr. 38: 10. 1888 (!). Holotype, Bulgaria. Ost.-Bulgarien, massenhaft in der Bucht von Varna zwischen Pontus und Devno-See, bei Galata, 1886, *Bornmüller* (B, non vidi); isotypes (G, K, W).

*Lepidotrichum uechtritzianum* (Bornm.) Velen. & Bornm. Österr. Bot. Zeitschr. **39:** 324. 1889 (!). — Bornm. Bot. Centr. **41:** 163. 1890. — Velen. Fl. Bulg. 42. 1891; Suppl. Fl. Bulg. **1:** 27. 1898. — Aznavour, Bull. Soc. Bot. Fr. **64:** 165. 1897. — Schulz in Engler & Prantl, Nat. Pflanzenfam. II. **17b:** 495. *fig. 271, m–o.* 1936. — Hayek, Prod. Fl. Pen. Balc. **1:** 428. 1925. — Stoj. & Steff. Fl. Bulg. ed. 2. 532. *pl., p. 585.* 1948.

DISTRIBUTION AND HABITAT: Maritime sands along the coast of the Black Sea in Bulgaria; one coastal record from Asiatic Turkey. Fl. July–Aug. (–Sept.).

BULGARIA: Burgas, *Jablonowski* (PRC, *fide* Velen. 1898). TURKEY: A2(A), Prov. Istanbul, Bournov (Jum Burnu near Kartal), *Nemetz 178* (G, hb. B.V.D. Post).

The long, linear rosette leaves, with dentate or repand margins, of *Aurinia uechtritziana* are conferted on indurated caudices. The bases of these leaves are grooved, swollen, and fleshy during the growing season, and persistent for a number of years. In addition to these characters, *Au. uechtritziana* shares with the other species of *Aurinia* spherical buds, cup-shaped calyces, reduced cauline leaves, and very sparsely foliate, nearly scapose fertile stems. The recognition and correlation of these characters for *Au. uechtritziana*, show that there are no apparent reasons, especially as there are no differences in floral morphology, to maintain the monotypic genus *Lepidotrichum* distinct from *Aurinia*. Although the silicles of *Au. saxatilis*, *Au. leucadaea*, and *Au. rupestris* are compressed or rarely sub-inflated, the strongly inflated and turgid silicles of *Au. uechtritziana* are not unique in the genus. *Aurinia corymbosa* and *Au. petraea* also have turgid silicles whose valves are strongly and equally inflated. In the majority of species of *Aurinia* the petals are yellow; however, in *Au. rupestris* and *Au. uechtritziana* they are white.

The only Turkish record of *Au. uechtritziana* to date was considered previously (cf. Velen. 1898; Hayek, 1925) as coming from Turkey-in-Europe (Thrace). In the original publication of this record, however, Aznavour (1897) clearly states that the plant was collected near Kartal, a village on the Marmara Sea on the Asiatic side of the Bosphorus. This collection, unfortunately, is only a portion of an inflorescence, but the

floral and indumentum characters indicate that it may be correctly referred to *Au. uechtritziana*.

3. **Aurinia rupestris** (Ten.) Cullen & Dudley, comb. nov.

Subsp. **rupestris**

*Alyssum rupestre* Ten. Prod. Fl. Nap. **1:** 37. 1811 (!). Holotype, Italy. In fissuris rupium Magellae (Mugellae a Sarimaravallo), *Tenore* (NAP, non vidi); isotype (G–DC). — Ten. Cat. Pl. Hort. Neap. **1:** 57. 1815; Fl. Nap. **2:** 72. *t. 60.* 1820; Syll. Fl. Neap. 316. 1831. — DC. Syst. Nat. **2:** 319. 1821. — Bertol. Fl. Ital. **6:** 498. 1844. — Fiori & Paol. Fl. Anal. Ital. **1:** 458. 1898; Ic. Fl. Ital. **1:** 166. *fig. 1451.* 1899.

*Koniga rupestris* (Ten.) Heyn. Nom. Bot. Hort. **1:** 439. 1840 (!).

*Lobularia rupestris* (Ten.) Steud. Nom. Bot. ed. 2. 68. 1841 (!).

*Koniga scardica* Griseb. Spic. Fl. Rum. & Bith. **1:** 278. 1843 (!). Holotype, Albania. In regione alpina Scardi: sparsim in pratis m. Kobelitza, alt. 1524–2134 m., *Grisebach* (GOET, non vidi); isotypes (G, K).

*Ptilotrichum rupestre* (Ten.) Boiss. Fl. Or. **1:** 288. 1867 (!). — Hal. Consp. Fl. Gr. **1:** 87. 1900. — Hayek, Prod. Fl. Pen. Balc. **1:** 442. 1925.

*Ptilotrichum rupestre* var. *scardica* (Griseb.) Hal. *loc. cit.* (!).

DISTRIBUTION AND HABITAT: An alpine confined to calcareous screes in Italy, Yugoslavia, Albania and Greece; alt. (500–) 1850–2700 m.

ITALY: Aprutii, Morrone, 1819, *Gussone* (G–DC); Morrone (fr.), monte Majella loca la Cimanera (fl.), 500–2000 m., July 1905, *Rigo* (BM, E, GH, K, W); Aprutio, Mont. Moroni et Majella, 1524–1829 m., 30 July 1874, *Porta & Rigo* (BM, E, GH, K, W); Aprutii, mont. "La Majella" et "Morrone", *Rigo 3908* (BM, E, GH, K); monte Amaro, 1819, *Schouw* (G–DC); Prov. de Chieti, monte Majella, inter mont. Amaro, 2700 m., *Fiori 1281* (BM, E, GH, K); Mt. Majella, *Boissier* (BM, G, GH, K). ALBANIA: Lunxherie, 1800–1900 m., *Lemperg 1406* (E, GH, K, W); Nemerzka, 2100 m. (haufiger), 1850–2100 m. (selten), *Lemperg 786* (E, GH, K, W); Nordost-Albanien, dist. Luma, Galica Lums, *Dörfler 705* (A, BM, E, K, GH, W); Koritnik, 2200 m., *Dörfler 605* (BM, E, K, GH, W).

The features which indicate that *Alyssum rupestre* and *Ptilotrichum cyclocarpum* (subsp. *cyclocarpa*) should be treated as components of *Aurinia*, rather than of *Alyssum* (or *Ptilotrichum* which is a synonym of *Alyssum*) are the major diagnostics of *Aurinia*. These characters are: spherical buds; cup-shaped calyces; long and narrow rosette leaves, with deeply grooved petioles having swollen and persistent bases conferted and rosulate on indurated caudices; very reduced cauline leaves; and sparsely foliate, nearly scapose fertile stems. *Aurinia rupestris* differs from the other species of the genus in having simple racemes.

Subsp. **cyclocarpa** (Boiss.) Cullen & Dudley, comb. & stat. nov.

*Ptilotrichum cyclocarpum* Boiss. Ann. Sci. Nat. Paris, II. **17:** 159. 1842 (!). Holotype, Turkey. B7: Prov. Tunceli, Kurdistan (Mounzur Dagh), *Aucher*

*279 bis* (G, non vidi); isotype (K). — Boiss. Fl. Or. **1**: 288. 1867. — Grossh. Fl. Kavkava. ed. 2. **4**: 211. 1950.

DISTRIBUTION AND HABITAT: An alpine endemic of Turkey, from the Cilician Taurus, the Anti-Taurus, and the Armenian Highlands; dry limestone ridges and screes; alt. 2000–2800 m. Fl. May–Aug.

TURKEY. A7, Prov. Gümüşane, Karahissartasch (near Elias dağ), 1894, *Sintenis 5505* (BM, E, GH); Gümüşane, *Bourgeau 33* (BM, E, GH, K, W); Ardas (Torut)–Besklise, *Sintenis 92* (E, W). A8, Prov. Gümüşane Erzurum, Bayburt-Erzurum, 1500 m., *Huet* (E, GH, W). B5, Prov. Kayseri, Bakir dağ, near Akoluk Yayla, 2500–2700 m., *Davis 19346* (BM, E, K). B6, Prov. Kayseri, Pinarbasi, 2000 m., *Stainton 5167* (E, K); Prov. Maraş, Berit dağ, 2800 m., *Balls 1087* (BM, E, K); dist. Göksun, Binboga dağ, above Yalak, 2000 m., *Davis 19977* (BM, E, K); 2200–2300 m., *Davis 20155* (BM, E, K); Isik dağ, above Karli Yayla, 2800 m., *Davis 20021B* (BM, E, K). B7, Prov. Tunceli, Munzur dağ, above Ovacik, 2800 m., *Davis 31241* (BM, E, K). C2, Prov. Burdur, Eldirek dağ, south of Dirmil, chalk, 1850–1920 m., *Huber-Morath 8451* (HM). C5, Prov. Içel/Niğde, Kysil depe above Bulghar Maaden, 2800 m., *Siehe 457* (BM, E); Bulghar Magara, 2600 m., *Siehe 573* (E, K); Bulghar Maaden, *Balansa 418* (E, K); Gysil depe-Ketsiebele, 2580 m., *Kotschy 126c* (E, W).

The only consistent difference between the Italian and Balkan subsp. *rupestris*, and the Anatolian subsp. *cyclocarpa*, is that the fruits of the latter, even in the immature state, are always glabrous. The fruits of subsp. *rupestris* have an indumentum, at least when immature. This constant difference, in conjunction with completely allopatric distributions, justifies the retention of the Turkish taxon at subspecific rank. A number of specimens from Albania and Greece link the two subspecies morphologically. The mature fruits of these intermediate specimens (often determined as *Koniga scardica* or *Ptilotrichum rupestre* var. *scardicum*) are glabrous, as are the mature fruits of the Turkish subsp. *cyclocarpa*. Their immature fruits, however, have an indumentum characteristic of that which is persistent on the fruits of the strictly European subsp. *rupestris*. This pattern of variation could be interpreted as an interrupted cline.

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# A RE-EVALUATION OF THE GENUS AMBROSIA (COMPOSITAE) [1]

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IN SPITE OF THE FOCUS in recent years on the ragweeds and their relatives as sources of allergenic pollen, they are poorly understood biologically and taxonomically. Systematic controversy has centered particularly about the question of the possible congeneric nature of the so-called "true ragweeds," *Ambrosia* spp., and "false ragweeds," *Franseria* spp. Linnaeus (1753) established the genus *Ambrosia* for modern use with the description of four species, *Ambrosia trifida*, *A. elatior*, *A. artemisiifolia* and *A. maritima*, all of which were based upon earlier descriptions. Cavanilles (1793) established the closely allied genus, *Franseria*, with the description of the single species *F. ambrosioides*. The similarity of the two genera was recognized by Cavanilles, as is shown by the specific epithet (*ambrosioides*) he chose for his species and by a statement in the description that he considered the new genus to be intermediate between the ragweeds (*Ambrosia*)

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and the cockleburs (*Xanthium*), "*genus mediam inter Ambrosiam et Xanthiam*" (p. 78). Since the time of Linnaeus and Cavanilles, as we have continued to explore and catalog the floras of the New World, the close affinity of these genera has become ever more apparent, and numerous instances of confusing intermediacy have been remarked between them. This is exemplified by a statement made by T. S. Brandegee, in 1889, in his description of *Franseria acuminata*: "This is *another* of the forms which *too closely* connects the genus with *Ambrosia*" (p. 171, italics mine). Recently Shinners (1949) reviewed the genus *Franseria* for central Texas, and stated, "This genus cannot be distinguished from *Ambrosia* except by mature fruit, and the difference . . . warrants the recognition of a subgenus at most" (p. 173). The work on ragweed biology undertaken at Michigan during the past several years (Gebben, Payne and Wagner, 1963; Payne, 1962a, 1962b, 1963; Payne, Raven and Kyhos, 1964) has convinced me that Shinners is correct and has provided further evidence to support the hypothesis that *Ambrosia* and *Franseria* are, indeed, congeneric. It is the purpose of this paper to present the evidence and to make the necessary nomenclatural changes.

The species of "ambrosioid" and "franserioid" ragweeds are wind pollinated composites with highly specialized inflorescences (Payne, 1963). The floral heads are unisexual, and both staminate and pistillate heads are normally borne on the same plant. The involucral appendages (phyllaries) of the pistillate heads are fused about the enclosed pistillate florets or floret to form a hard, indehiscent conceptacle. The tips of the appendages are more or less evident as spiny processes which project from the surface of the involucre body at maturity. The number and arrangement of these spines provides the single criterion by means of which *Ambrosia* and *Franseria* have been distinguished. In *Franseria, sensu stricto,* the plants produce fruiting involucres that characteristically bear numerous spines scattered more or less uniformly over the surface, whereas fruiting involucres of *Ambrosia, sensu stricto,* are characterized as bearing few spines arranged in a single whorl below the involucral beak. This difference is superficial, however, when the variation of all of the species in these complexes is considered. The spines of the pistillate involucres of species such as *Ambrosia artemisiifolia, A. trifida,* and *A. psilostachya* are arranged, in many instances, not in a single whorl, but in two, three, or more, few-spined whorls compacted near the apex of the fruiting involucre body. Intermediate involucral forms are encountered among specimens of a wide variety of franserioid species; fruiting involucres representative for both genera are commonly found among members of the *Franseria confertiflora, F. acanthicarpa,* and *F. canescens* complexes, and species such as *F. bryantii* and *F. linearis* can be placed almost equally well in either genus. Numerous "intergeneric" synonyms are found in the literature which reflect this morphologic interdigitation, and the ambiguity and lack of constancy of the character state used to distinguish *Ambrosia* from *Franseria* constitutes, in itself, as noted by Shinners (op. cit.), a compelling argument for combination of the two.

Furthermore, I have produced an "intergeneric hybrid" in the greenhouse between the two very distinct species *Ambrosia artemisiifolia* (seed parent, $n = 18$) and *Franseria acanthicarpa* (pollen parent, $n = 18$). Morphological features of the parental species and of the hybrid $F_1$ are illustrated in TEXT-FIG. 1. Consideration of the hybrid series thus initiated lends additional support for combination. Chromosome pairing in the hybrid was observed to be very good; many configurations consisted of 18 bivalents at diakinesis, while others showed only one or two pairs of univalents (TEXT-FIG. 1D). Pollen viability, as estimated by staining in acetocarmine, was approximately 30 per cent. Seeds, formed in abundance, were 40 per cent germinable and produced a vigorous $F_2$. At the time of writing, the series had been carried through the $F_3$ generation (pollen viability of individual specimens, 57 to 94.5 per cent; mean viability for 19 specimens, 81.5 per cent; seed viability for two selected seed lots, 63.3 per cent and 96 per cent), and $F_4$ progeny were growing in the greenhouse. While the occurrence of intergeneric hybridization is not, in itself, of great taxonomic significance, the high degree of chromosomal compatibility and genome homology demonstrated by this hybrid series does not support separation of the parental species in different genera.

Still further support for the union of *Ambrosia* and *Franseria* may be derived from a consideration of the evolutionary relationships of the species or species groups involved. Since the ragweeds, *sensu lato*, comprise a large and morphologically diverse group, numerous characteristics may be analyzed to indicate relative species advancement and relationships. Progressions from primitive to advanced character states which have been worked out within the group include the following:

HABIT

1. From shrubs to perennial herbs and annuals.

LEAVES

1. From petiolate to sessile.
2. From alternate to opposite.
3. From pinnately lobed to palmately lobed or unlobed.
4. From heavily pubescent and somewhat coriaceous to less pubescent and membranaceous.

STAMINATE CAPITULA

1. From stalked to sessile.
2. From capitulous stalks which bear more than one head to one-headed stalks.
3. From centric attachment of the stalk to the involucre to eccentric attachment.
4. From well defined involucral lobes (phyllary tips), separated by deep sinuses, to involucral lobes which are poorly defined or lacking.
5. From large heads with many florets to small heads with few florets.

PISTILLATE CAPITULA

1. From several florets to a single floret per capitulum.
2. From many and scattered (imbricated) spines to few and localized spines.

TEXT-FIG. 1. *Ambrosia artemisiifolia* × *"Franseria" acanthicarpa*. Representative leaves (subscript 1), staminate involucres (subscript 2) and fruiting involucres (subscript 3) for: A, *F. acanthicarpa*, pollen parent, $n = 18$; B, *A. artemisiifolia*, seed parent, $n = 18$; C, the hybrid (superscript numerals denote nodes from which leaves were removed). D, Meiotic chromosome figures drawn from hybrid material (voucher: *Payne AVS-3346*, MICH): $D_1$ through $D_3$, configurations demonstrating perfect pairing (18 bivalents); $D_4$, configuration showing 4 univalents; $D_5$, configuration showing 2 univalents. The line to the upper right is equivalent to 10 cm. for leaf silhouettes and 10 mm. for involucre drawings.

3. From flat and strongly emergent (phyllary like) spines to terete spines. Secondary modification has given rise to hooked and vestigial spines.

Although the details of evolutionary pathways must still be worked out in many instances, the character progressions cited above, together with simple, nonprogressional similarities, can be used to assess relative advancement and to indicate infrageneric groupings and relationships. In general, species of *Ambrosia, sensu stricto,* appear to be more advanced than, and to have been derived from, species or species groups of *Franseria, sensu stricto.*

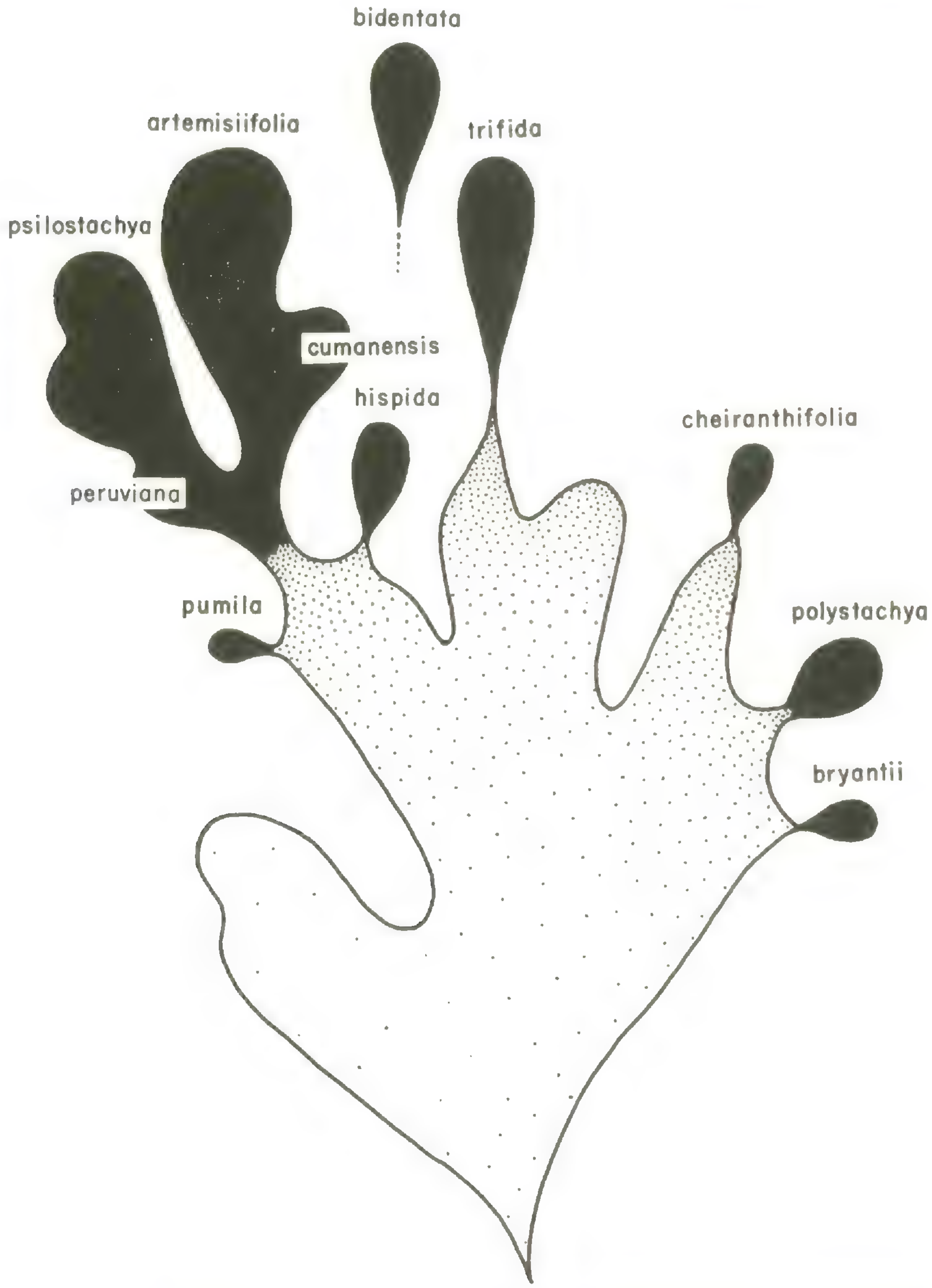
Rydberg (1922) recognizes 15 subgeneric groups among the species of *Ambrosia* and *Franseria*; however, his distinctions are often somewhat slight, serving better to distinguish small parcels of related species than to point out significant groups of evolutionarily related organisms. For the present purposes, therefore, I shall recognize three major subgeneric complexes, two of which include both franserioid and ambrosioid members, and a fourth containing only *Ambrosia bidentata.* These may be characterized as follows:

1. A central or core group, comprised of the majority of the species and characterized by usually quite pubescent (especially on the lower surface), pinnately to tripinnately lobed leaves. The group is, in itself, highly complex, with evolutionary lines apparently leading from the least specialized, shrubby, franserioid species, such as *Franseria dumosa* and *F. eriocentra,* along several derivative pathways to ambrosioid species as follows: To *Ambrosia trifida* along a line characterized by species with striated staminate involucres and nonhooked spines; the closest relatives of *A. trifida* probably include *F. chamissonis* and *F. acanthicarpa.* To *A. cheiranthifolia* through herbaceous species with less lobed, "bicolored" leaves, such as *F. linearis.* To *A. bryantii* via a shrubby line with much divided, irregularly lobed leaves, including such species as *F. camphorata* and *F. magdalenae,* predominant in Baja California, Mexico. To the South American species, A. *polystachya,* through the remarkably similar *F. artemisioides* Willd.

2. A small, derivative group, found in the desert regions of the southwestern United States and western Mexico, made up of shrubby species which are characterized by unlobed (or nearly so) leaves, a heavily glandular indument, and fruiting involucres which closely resemble those of *Xanthium*, the cockleburs. This subgroup includes *Franseria ambrosioides, F. ilicifolia, F. chenopodiifolia* and *F. deltoidea.* This complex displays no obvious, direct affinities with any of the ambrosioid species, although it is connected to franserioid members of group 1, above, and may be closely related to the *Xanthium strumarium* (*sensu lato*) complex.

3. A highly specialized, derivative group of perennial herbs and annuals which are characterized by membranaceous, regularly pinnately to tetrapinnately lobed leaves and small staminate and pistillate involucres, the former without striations and the latter usually one-flowered and with reduced spines. This complex includes *Franseria canescens* and *F. confer ti-*

*flora*, which appear to be related to ambrosioid species as follows: *F. canescens* is probably closely related to the very similar *A. pumila*, the latter being smaller in stature and with reduced fruit spines. *Ambrosia hispida*, a species of the Caribbean strand, closely resembles *A. confer-*




TEXT-FIG. 2. Schematic representation of the polyphyletic nature of *Ambrosia*, ***sensu stricto***. The stippled body represents the franserioid assemblage; black lobes represent ambrosioid species or species groups, as indicated, which have been derived from it.

*flora*, having more hispid leaves, reduced fruit spines and a slightly different habit. The large and highly integrated ambrosioid complex which includes *A. artemisiifolia*, *A. cumanensis*, *A. peruviana* and *A. psilostachya*, is probably connected to *A. confertiflora* along a different line from that which leads to *A. hispida*, through intermediate species such as *A. velutina* and *A. tenuifolia* Spreng.

4. A fourth group containing the single species *A. bidentata*, the relationships of which are obscure, can be recognized. This is one of the most highly specialized of the ragweeds, with sessile, unlobed (but basally toothed) leaves, medium-sized, one-flowered pistillate involucres with few spines, and sessile staminate involucres with extreme prolongation of the distal lobe. It hybridizes easily with *A. trifida* and shares with it the annual habit, relatively large fruiting involucres and the condition of aneuploidy, but displays none of the morphological peculiarities characteristic of *A. trifida*. On the latter basis, it would appear to be more closely related to group 3, above, but its progenitor cannot be distinguished at present.

The relationships suggested in the foregoing paragraphs are summarized diagrammatically in TEXT-FIG. 2, in which the franserioid complex is represented as a stippled, lobed mass and the derivative, ambrosioid complexes are shown as black, peripheral lobes. This arrangement is supported by the distributional pattern obtained by designating three artificial groups containing the apparently most primitive species, the intermediate species, and the most advanced species. The first group is located in the desert Southwest, the second in less arid regions surrounding it, and the third extends to the northern and eastern periphery of the *Ambrosia-Franseria* range, providing a classic picture of the diversification and outward spread from a center of origin of ever more advanced members of a genus. It is evident that, if the suggested evolutionary lines are even approximately correct, *Ambrosia*, in the strict sense, is a highly polyphyletic group, its divisions involving as ancestral forms different members of *Franseria*, a situation which is unacceptable by present generic standards.

In view of the above arguments in support of combining *Ambrosia* and *Franseria*, including the poorly defined and undependable criteria for separating them, an apparently higher degree of genome and chromosome homology than is ordinarily found between distinct genera, and the polyphyletic nature of *Ambrosia, sensu stricto*, they are combined below, and the necessary nomenclatural changes are made in the following pages. The treatment of the species and the synonymy presented do not constitute a monograph of the genus as newly defined but are intended only to clarify the nomenclature of the "franserioid" members listed.

**Ambrosia** Linnaeus, Sp. Pl. 2: 987. 1753; Gen. Pl. ed. 5. 425. 1754, non *Ambrosia* sensu Hort. ex Bedevian, Ill. Polyglot. Dict. 170. 1936 (Chenopodiaceae). Type species: *A. maritima* L. Sp. Pl. 2: 988. 1753.

*Gaertneria* Medicus, Phil. Bot. 1: 45. 1789, non *Gaertnera* Schreb. 1789 (Mal-

phigiaceae), nec *Gaertneria* Neck. 1790 (Gentianaceae), nec *Gaertnera* Retz. 1791 (Campanulaceae), nec *Gaertnera* Lam. 1791 (Loganiaceae). Type species: *Ambrosia fruticosa* Medic. Hist. Comment. Acad. Elect., Theodoro-Palatinae **3:** 244. 1775, nomen illeg., *Ambrosia arborescens* Mill. 1768.

*Franseria* Cavanilles, Ic. Descr. Pl. **2:** 78. 1793, nomen cons., Int. Code Bot. Nomencl., Reg. Veg. **23:** 318. 1961. Type species: *F. ambrosioides* Cav. *Ibid.* NOTE: This name is erroneously equated in the Code (loc. cit.) with *Ambrosia arborescens* Mill. (1768), an error which may be based on the fact that *A. arborescens* Mill. is synonymous with *Franseria artemisioides* Willd. (1805) and there is, as a result, confusion between the epithets "artemisioides" and "ambrosioides."

*Hemiambrosia* Delpino, Studi Lign. Anem. Comp. Artem. 16. 1871. Type species: *H. heterocephala* Delp. *Ibid.*, nomen illeg., *Ambrosia pumila* (Nutt.) Gray 1882.

*Hemixanthidium* Delpino, *Ibid.* 17. Type species: *H. paradoxum* Delp. *Ibid.*, nomen illeg., *Ambrosia acanthicarpa* Hook. 1834.

*Xanthidium* Delpino, *Ibid.* 17. Type species: *X. tenuifolium* Delp. *Ibid.*, nomen illeg., *Ambrosia confertiflora* DC. 1836.

*Acanthambrosia* Rydberg, N. Am. Fl. **33:** 22. 1922. Type species: *A. bryantii* (Curran) Rydb., nomen illeg., *Franseria bryantii* Curran, 1888.

The genus *Ambrosia*, in the new sense, may be characterized briefly as follows: Shrubs or subshrubs to perennial herbs spreading by means of stem and (or) root proliferations, or strictly annual herbs. Entire plant glandular, aromatic with resinous odor, glandular trichomes (colleters) biseriate, sessile or long-stalked. Leaves diverse (often with considerable intraspecific variation), pinnately lobed or dissected, palmately lobed or unlobed, petiolate or sessile. Anemophilous; staminate and pistillate florets in distinct heads normally borne on the same plant. Staminate heads stalked to subsessile or sessile, borne in usually aphyllous, spicate or racemose clusters at the tips of stems and branches, the phyllaries laterally connate and forming a broadly funnel-shaped to cupulate or saucer-shaped involucre with the phyllary tips more or less prominent as marginal lobes; receptacle paleaceous, pales various; many to several flowered. Staminate florets modified: calyx or pappus lacking; corolla hyaline, campanulate, 5-lobed (rarely 4-lobed), only comissural veins present; stamens 5, alternating with corolla lobes, filaments sometimes connivent, anthers without "tails," weakly connivent, sometimes separating during pollen discharge, terminal appendages deltoid to long-attenuate; pistil reduced (pistillodium), ovary lacking, style short, truncate (stigmatic lobes lacking) with terminal, circular "brush" of hairs (penicillate). Pollen subglobose, echinate, the spines short, 3-pored (rarely 2–6-pored) with bladder-like air chambers developed within the exine between the pores. Pistillate heads borne in sessile or stalked clusters in axils of leaves subtending staminate racemes or spikes; bases of phyllaries fused to form a hard, vase shaped conceptacle; phyllary tips forming more or less spiny processes, straight or uncinate, flattened or terete, strongly emergent or vestigial, rarely lacking, variously arranged or scattered over surface of

fruiting involucre; without pales; florets few (6–7) to one, if more than one, interior of fruiting involucre compartmentalized, each floret in a separate chamber. Pistillate florets reduced: perianth lacking; androecium lacking; mature ovary obovate, base somewhat oblique, abruptly rounded to base of short style; stigmatic lobes elongate, linear, spreading, inner stigmatic surface minutely papillose, exserted through spine-like beaks at apex of involucre, several-flowered involucres usually with distinct beak for each stigma but occasionally with a communal beak.

Basic chromosome number, $x = 18$, the majority of species diploid but outbreeding populations of tetraploids, hexaploids, and octoploids known, in some instances within what are here considered single species; two aneuploid derivatives known, *A. bidentata* ($n = 17$), *A. trifida* ($n = 12$).

Predominantly New World, mostly North American, including species of arid and semi-arid habitats and weedy species of ruderal sites.

Virtually all species exhibit extreme morphological variability. In numerous instances variants which appear to be within the natural limits of variation for given species have received separate names. Measurements cited in the species descriptions which follow are usually given as maxima found in non-teratological specimens from populations growing under favorable conditions.

1. **Ambrosia acanthicarpa** Hook. Fl. Bor. Am. 1: 309. 1834. Type: Banks of the Saskatchewan and Red River; *Douglas* (probably in K but not seen). NOTE: Although I have not seen the type, Douglas' description leaves no doubt of its identity. Among other characters Douglas refers to the bipinnatifid leaves and the "singularly spinescent fruits," the fruit spines being long, rigid and subulate. No other species from the northwestern United States displays this combination of characteristics.

*Franseria montana* Nutt. Trans. Am. Phil. Soc. ser. 2. **7:** 345. 1840. Type: In Rocky Mountains. near the Colorado of the West, *Nuttall* (possibly in BM [not seen] or PH!; isotype, GH!).

*Franseria hookeriana* Nutt. *Ibid.* Type: Based upon *Ambrosia acanthicarpa* Hook.

*Hemixanthidium paradoxum* Delp. Studi Lign. Anem. Comp. Artem. 17. 1871. Type: Based upon *Franseria montana* Nutt.

*Gaertnera hookeriana* (Nutt.) Kuntze. Rev. Gen. Pl. **1:** 339. 1891.

*Franseria acanthicarpa* (Hook.) Cov. Contr. U.S. Nat. Herb. **4:** 129. 1893.

*Gaertnera acanthicarpa* (Hook.) Britt. Mem. Torrey Club **5:** 332. 1894.

*Franseria californica* Gandoger, Bull. Soc. Bot. Fr. **65:** 54. 1918, non *Ambrosia californica* Rydb. 1922. Type: California, ad San Bernardino, *Parish*, October, 1893 (US!).

*Franseria palmeri* Rydb. N. Am. Fl. **33:** 25. 1922. Type: California, San Diego, *Dr. E. Palmer*, 1875 (US!).

Erect, annual herb, to 15 dm. high, becoming much branched. Leaves opposite below, alternate above, petiolate, petioles to 6 cm. long, laminar tissue narrowly decurrent to base. Lamina extremely variable, broadly

deltoid to narrowly lanceolate; to ca. 8 cm. long and 6 cm. broad, pinnately to tripinnately lobed, lobes from narrowly linear to subovate and abruptly acute; both surfaces green, sparsely tomentulose to strigose or hispid-scabrous. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 15 mm. long, usually shorter, 3–12 mm. broad, 3–9-lobed, lobes shallow to well-defined with sinuses separating lobes reaching halfway or more to point of stalk attachment, upper surface of three distal lobes usually marked with heavy, black striations along midveins. Fruiting involucres in sessile clusters below staminate racemes, to 10 mm. long and 14 mm. wide, 1-flowered; spines to 30, flattened, linear to lanceolate, sharply pointed, to 8 mm. long, scattered, occasionally vestigial or lacking. Haploid chromosome number, $n = 18$.

Flowering: June to December.

Range: Prairie and semi-arid regions of the western United States, from the Dakotas, Nebraska and Kansas, west to New Mexico, Arizona, California, Washington and Oregon. Adventive in eastern Minnesota.

Notes: As here circumscribed, this is one of the most heteromorphic of the ragweeds. Most segregates have been delimited on the basis of leaf and fruit spine differences which do not appear at present to be sufficiently correlated to permit recognition of distinct taxa within the complex.

2. **Ambrosia acuminata** (Brandeg.) Payne, comb. nov. PLATE I

*Franseria acuminata* Brandeg. Proc. Calif. Acad. ser. 2. 2: 171. 1889. Type: Mexico, Lower California, Purísima [Purissima]. *T. S. Brandegee*, February 11, 1889 (UC, no. 88798; NY, photograph!; isotype, US! no. 47364).

Erect shrub, probably over 3 dm. high. Leaves alternate, petiolate, petiole to 18 mm., laminar tissue narrowly decurrent to base, usually with one or more pairs of small lobes below the main laminar region. Lamina lanceolate to ovate-deltoid in outline; to 8 cm. long, pinnately lobed, somewhat irregular, rachis of the lamina broad above first sinus, terminal lobe large, attenuated and comprising major portion of blade. Staminate involucre stalked, stalks to 5 mm. long, lowermost stalks sometimes bearing more than one head, involucre to 3 mm. broad, cupulate; marginal lobes 3–7, shallow. Fruiting involucre to 6 mm. long and 3 mm. broad, 2-flowered; spines few (ca. 4–8), less than 1 mm. long, uncinate, appressed, scattered. Chromosome number unknown.

Flowering: February.

Range: Baja California, Mexico, known only from the type specimen.

3. **Ambrosia ambrosioides** (Cav.) Payne, comb. nov. PLATE I

*Franseria ambrosioides* Cav. Ic. Descr. Pl. 2: 79. 1793. Type: Not seen, probably at MA. The description of this species is based upon material cultivated at the Royal Bot. Gard., Madrid, and represented by Plate 200, Cav., loc. cit. This plate is very well done and, in view of the unusual morphology of this species, leaves no question as to the identity of the taxon.

*Xanthidium ambrosioides* (Cav.) Delp. Studi Lign. Anem. Comp. Artem. 18. 1871.
*Gaertnera ambrosiodes* (Cav.) Kuntze, Rev. Gen. Pl. **1:** 339. 1891.

Erect shrub, to 25 dm. high. Leaves alternate, petiolate, petiole to 8 cm. long, usually without obvious decurrent tissue from the lamina. Lamina lanceolate-attenuate (rarely to ovate) 2–18 cm. long or longer, 1–6 cm. wide, unlobed or with marginal teeth developed as weak lobes, both surfaces bright green, tomentose, glandular, sticky when fresh with a strongly resinous odor. Inflorescence racemose, usually much branched below. Staminate involucres stalked, stalks to 14 mm., the lower often bearing more than one head; involucre to 8 mm. broad, lobes 7–12, teeth prominent, sinuses extending 1/3–1/2 way to point of stalk attachment, midveins of lobes darkened upon drying, occasionally marked with obscure striations on upper surface. Fruiting involucre to 15 mm. long and 12 mm. broad, florets 3–5; spines numerous, usually more than 30, scattered thickly over surface of involucre, slender, uncinate, 2–4 mm. long; mature involucres closely resembling those of *Xanthium*, the cocklebur. Haploid chromosome number, $n = 18$.

Flowering: February to May.

Range: Sonoran Desert region, common through southern Arizona, extending into San Diego County, California, and to Sonora and Baja California, Mexico; rare in the Mexican states of Sinaloa and Coahuila.

Notes: The type species of *Franseria*, as mentioned earlier, was erroneously synonymized with *A. arborescens* Mill. in the *International Code of Botanical Nomenclature*, Reg. Veg. **23:** 318. 1961, probably through equation with *F. artemisioides* Willd. which is synonymous with *A. arborescens* Mill.

4. **Ambrosia arborescens** Mill. Gard. Dict. ed. 8. 1768, non *Franseria arborescens* Brandeg. 1903. Lectotype: Garden specimen from Philip Miller collections (BM; photograph MICH!, BH, negative no. 5274). PLATE II

*Ambrosia fruticosa* Medic. Hist. Comment. Acad. Elect., Theodoro-Palatinae 3: 244. 1775, non *Ambrosia fruticosa* DC. 1836, nec *Franseria fruticosa* Phil. 1891. Type: not designated. NOTE: Medicus' Plate 20 provides a very good illustration of this species, which, together with the description, in which the species is equated with *A. arborescens* Mill., leaves no question as to the identity of the taxon.

*Xanthium fruticosum* L.f. Suppl. Plant. Syst. Veg. 418. 1781. Type: Based upon *A. arborescens* Mill. NOTE: This name change was apparently made because of the somewhat *Xanthium*-like fruiting involucres of the species and the seeming impossibility of including a plant with such fruits in *Ambrosia* as delimited at that time.

*Ambrosia frutescens* Lam. Encyc. Meth. **1:** 128. 1783, *in synon.*

*Franseria artemisioides* Willd., Linn. Sp. Pl. ed. 4. **4:** 378. 1805, non *Ambrosia artemisioides* Meyen & Walp. ex Meyen, 1843. Type: Based upon *Xanthium fruticosum* L.f. and upon *Ambrosia arborescens* Mill. as described by

Lamarck (loc. cit.). NOTE: A tracing of material of this species from the Willdenow collections (B) was made by F. W. Klatt before 1898 and is now in GH!.

*Xanthidium artemisioides* (Willd.) Delp. Studi Lign. Anem. Comp. Artem. 18. 1871.

*Gaertnera artemisiodes* (Willd.) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

*Franseria conwayi* Rusby, Bull. N.Y. Bot. Gard. 8: 130. 1912. Type: Bolivia, Santa Cruz, *R. S. Williams 1464*, Aug. 25, 1902 (NY!).

Erect shrub, to 40 dm. high. Leaves alternate, petiolate, petioles to 10 cm. long, laminar tissue decurrent to base, several small lobes usually formed below main lamina. Lamina ovate-lanceolate to broadly ovate, deltoid or nearly orbicular in outline, to 20 cm. long and 24 cm. wide, bi- or tripinnately lobed, the second or third order lobes intergrading with the laciniate-serrate marginal teeth; upper surface green, puberulous to glabrate, lower surface gray-green, woolly-tomentose. Inflorescence paniculate-racemose, lower staminate stalks often with several heads. Staminate involucre stalked, stalk to 10 mm., often much shorter, involucre to 6 mm. broad, 5–9-lobed, sinuses between lobes often extending more than ½ way to point of stalk attachment; veins on upper surface of lobes darkened, sometimes with black striations near tips. Fruiting involucres in often massive, sessile clusters below the staminate heads, 5–8 mm. long, 4–7 mm. broad, body thick and heavy, often nearly black, (1)2–4-flowered, stigmas discharged through a communal beak or through poorly defined distinct beaks; spines 12–20, scattered over surface, 1–3 mm. long, bases thick, abruptly narrowed to slender, uncinate tips, somewhat appressed. Chromosome number unknown.

Flowering: Throughout year.

Range: Interandean plains of Ecuador, north to north-central Colombia, south through Peru to western Bolivia.

Notes: A variable species in regard to habit, leaf size, and morphology. *Franseria conwayi* appears to be based upon a specimen with aberrant leaves. *Ambrosia arborescens* is apparently a plant well known to the inhabitants of the regions in which it occurs (colloquial name "Altimisa," sometimes erroneously transliterated to "Artemisia"). Notes of W. H. Camp (specimens *E-2498* and *E-5030*, NY) contain the following remarks "'it is good to sweep out a house which has too many fleas' . . . it seems to be the only thing used to sweep out ovens after heating and before the bread is put inside. It is sold on the Cuenca [Ecuador] market for this purpose . . . Used as a local application in skin infections." This widespread use may explain arrival of the species in Europe early enough to be included in Miller's *Gardeners Dictionary*.

5. **Ambrosia artemisioides** Meyen & Walp. ex Meyen, Nov. Act. Acad. Caes. Leopold. Carol. 19 (suppl. 1, Nat. Cur., Obs. Bot.): 268. 1843, non *Franseria artemisioides* Willd. 1805, nec *Xanthidium artemisioides* (Willd.) Delp. 1871, nec *Gaertnera artemisiodes* (Willd.) Kuntze, 1891. Neotype: Peru, Tacna, Maisin, in glareosis joropi, *Lechler*

*1568*, in 1854 (NY!; duplicate in GH). NOTE: The Meyen and Walpers material upon which this taxon was based (Peru: in planitie circa Tacoram, alt. 14–17,000 ped.) was presumably destroyed in Berlin during World War II. Their description is, however, diagnostic "Plant shrubby, erect, pilose, branched; all leaves narrowly linearly pinnatifid, lobes obtuse, entire to pinnately incised, scarcely puberulent, . . . rachis . . . barely 1/2 a line wide, roundish . . . ; fruiting involucre spiny, spines uncinate; stem . . . strongly glutinous." The fact that Hohenacker evidently examined their material in Berlin and equated it with the Lechler specimen which is the type for the following synonym, provides a basis for acceptance of Meyen's name for this species and for the selection of Lechler's specimen as the neotype. PLATE I

*Franseria meyeniana* Sch. Bip. ex Hohenacker, Bonplandia **4**: 54. 1856. Type: *Lechler 1568* (as above) (W, not seen; isotypes GH, NY!).

*Franseria fruticosa* Phil. Anal. Mus. Nac. Chile, seg. secc. Botanica. 50. 1891, non *Ambrosia fruticosa* Medic. 1775, nec *Xanthium fruticosum* L.f. 1781, nec *Ambrosia fruticosa* DC. 1836. Type: Chile, Tarapaca, *Philippi*, 1888 (B, not seen; photograph, GH!).

*Gaertnera meyeniana* (Sch. Bip.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

*Franseria recurva* Rusby, Bull. N.Y. Bot. Gard. **8**: 131. 1912. Type: Peru, Arequipa, 7500 ft., *Rusby 2527*, Aug. 8, 1901 (NY!; isotype US! no. 1098696).

Erect shrub, becoming much branched, new growth stem tending to be brown-black, glutinous, somewhat pilose, bark of older stem gray, lacking pubescence. Leaves alternate, petiolate, petioles to 4 cm. long (usually much shorter) laminar tissue decurrent to base. Lamina ovate in outline to 4 cm. long and 3 cm. wide, irregularly bipinnately lobed, lobes linear; both surfaces green, sparingly puberulent to glabrate, minutely glandular. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 8 mm. long, occasionally more than one head borne on lower stalks, involucre to 5 mm. broad, 7–12-lobed, lobes often marked with black striations along midveins, sinuses separating lobes extending ca. 1/2 way to point of stalk attachment. Fruiting involucres in small axillary clusters below staminate capitula, 4–6 mm. long, 2–3 mm. wide, 1(?)-fruited; spines to 20, scattered, slender, uncinate, to 2.5 mm. long, easily broken from body. Chromosome number unknown.

Flowering: March to August.

Range: Southern Peru (Arequipa province) to northern Chile (Tarapaca province).

Notes: I have seen only six specimens of this species, including the types, and these display considerable leaf variation, tending to merge with what seems to be an undescribed species of the same area with larger, more broadly lobed leaves, larger staminate heads and fruiting involucres of quite different morphology, viz. *F. W. Pennell 13107* (NY), *Mr. & Mrs. F. E. Hinkley 79* (NY). The spines of the fruiting involucre of *A. artemi-*

*sioides* appear to be easily broken from the body at an abscission zone, a characteristic unknown elsewhere in the genus.

6. **Ambrosia bryantii** (Curran) Payne, Madroño **16**: 234. 1962.
*Franseria bryantii* Curran, Proc. Calif. Acad. ser. 2, 1: 232. 1888. Type: Mexico, Baja California, Magdalena Bay, Santa Margarita Island, *Walter E. Bryant*, in 1888 (CAS, not seen; isotype, UC). NOTE: Although I have not examined the type material of this species, Dr. Elizabeth McClintock (CAS) and Miss Annetta Carter (UC) have kindly verified its nature and location. Both of the specimens cited probably comprise the original holotype and they have been labelled respectively "part of the type" and "part of type" by Mrs. Curran who, at the time *Franseria bryantii* was published, was the editor of the *Proceedings*, and a member of the staff of the California Academy of Sciences. It is assumed that the material was divided and incorporated into the T. S. Brandegee collections at the University of California after Mrs. Curran's marriage to Brandegee. It is, therefore, appropriate to consider the CAS material as the holotype.

*Acanthambrosia bryantii* (Curran) Rydb. N. Am. Fl. 33: 22. 1922.

Erect shrub, reaching ca. 8 dm. Leaves alternate, petiolate, petioles to 3 cm. long, laminar tissue decurrent to base, usually forming several small lobes below main laminar region. Lamina ovate in outline, to 8 cm. long and 6 cm. broad, irregularly bi- to tripinnately lobed, lobes linear; both surfaces green, lower becoming lighter, nearly glabrous to sparsely hispidulous. Inflorescence racemose-spicate. Staminate involucres subsessile to stalked, stalks to 2 mm. long; involucre to 7 mm. broad, 8–12-lobed, lobes shallow, not noticeably striate. Body of fruiting involucre to 10 mm. long and 5 mm. broad, 2–7-flowered, the stigmas discharged through a common beak; spines 5–9, chalk-white, 12–40 mm. long, sharp, clustered near apex of involucre body. Haploid chromosome number, $n = 18$.

Flowering: February to April.

Range: Central to southern Baja California, Mexico.

Notes: A species remarkable for the long, thorny spines of the fruiting involucre, and for retention of a percentage of the fruiting involucres to function as armature through several growing seasons. Segregated in the monotypic genus *Acanthambrosia* by Rydberg because of the discharge of the stigmatic lobes of all contained florets through the single beak, a phenomenon also displayed by other species.

7. **Ambrosia camphorata** (Greene) Payne, comb. nov. PLATE III

*Franseria hispida* Benth. in Hinds, Bot. Voy. Sulphur, 25. 1844, non *Ambrosia hispida* Pursh, 1814. Type: Mexico, Lower California, Magdalena Bay, Barclay (K, not seen; ARIZ! photograph; GH! drawing of type by Smith, July 4, 1919).

*Franseria bipinnatifida* sensu Gray ex Wats. Proc. Am. Acad. **11**: 115. 1876, non *Franseria bipinnatifida* Nutt. 1840, nec *Ambrosia bipinnatifida* (Nutt.)

Greene, 1894. Mexico, Baja California, Guadalupe Island, *E. Palmer 40*, in 1875 (NY!; PH!).

*Franseria camphorata* Greene, Bull. Calif. Acad. **4:** 192. 1886. Type: Mexico, Lower California, Guadalupe Island, *E. L. Greene*, April 24, 1885 (CAS, not seen; isotype, NY!).

*Franseria camphorata* var. *leptophylla* Gray, Proc. Am. Acad. **22:** 309. 1887. Type: Mexico, Lower California, near San Fernando, *C. R. Orcutt 1352*, May 4, 1886 (US!).

*Gaertnera hispida* (Benth.) Kuntze, Rev. Gen. Pl. **1:** 339. 1891. NOTE: Kuntze credits the original name to "Barcl.," a misconception probably resulting from the fact that the type of *F. hispida* Benth., collected by Barclay, is labelled "*Franseria hispida* sp. n. Barclay."

*Franseria leptophylla* (Gray) Rydb. N. Am. Fl. **33:** 32. 1922.

Erect shrub, becoming much branched from the base; to 6 dm. tall; glandular throughout, viscid-sticky when fresh, with strongly resinous odor. Leaves alternate, petiolate, petioles to 10 cm. long, usually shorter, laminar tissue decurrent to base, usually with several medium to small pairs of lateral lobes below main laminar region. Lamina deltoid-lanceolate to ovate or lanceolate in outline, to 10 cm. long and broad, irregularly bi- or tripinnately lobed, lobes various; upper surface gray-green to green, minutely glandular, sparingly puberulent to glabrate, lower surface gray-green to white woolly-tomentose. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 5 mm. long, involucre to 7 mm. broad 7–12-lobed, upper surface of lobes often marked with obscure striations, sinuses separating lobes extending approximately halfway to point of stalk attachment. Fruiting involucres variable, 1–7-flowered, 5–10 mm. long, 3–11 mm. broad; spines 3–15 (rarely none), terete, variously arranged or scattered, strongly emergent to vestigial. Haploid chromosome number, $n = 36$.

Flowering: September to May.

Range: Throughout Baja California, sporadic in western Sonora and southern San Luis Potosi, Mexico.

Notes: An extremely variable species, especially in regard to fruiting involucre morphology; possibly an aggregate or with several intergraded varieties, needing further study.

8. **Ambrosia canescens** Gray, Proc. Am. Acad. **17:** 217. 1882. Type: Mexico, Aguas Calientes, In arvis communis, *Hartweg 121*, in 1839 (K; photograph MICH!, Kew negative number 715, 715 A; isotypes, GH, NY!). PLATE IV

*Ambrosia fruticosa* var. *canescens* Benth. Pl. Hartweg. 17. 1839, nomen nudum.

*Franseria canescens* (Gray) Rydb. N. Am. Fl. **33:** 27. 1922.

Erect perennial herb, perennating by means of shoots from roots. Leaves alternate, petiolate, petioles 1–5 cm. long, laminar tissue decurrent to base, often with 1 or more reduced pairs of lobes below main laminar region. Lamina broadly ovate to lanceolate in outline, to 8 cm. long and 6 cm. wide, finely bi-, tri- or tetrapinnately lobed; both surfaces gray-canescent.

Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 3 mm. long, involucre 3–6 mm. in diameter, 5–10-lobed, the sinuses shallow. Fruiting involucres 1-fruited, 3–6 mm. long, 2–5 mm. broad; spines 0–10, strongly emergent (to 2 mm. long) to vestigial, usually flattened, occasionally uncinate, variously scattered or grouped over surface. Haploid chromosome number, $n = 18$.

Flowering: April to October.

Range: East-central Mexico, from San Luis Potosi to Durango, south to Aguascalientes. Also reported from Chihuahua (*C. G. Pringle 1284*, GH, NY) and Arizona (*H. H. Rusby 680*, NY).

Notes: A species of considerable variability, appearing to intergrade somewhat with *A. confertiflora* in the eastern portion of its range.

9. **Ambrosia carduacea** (Greene) Payne, comb. nov. PLATE II

*Franseria arborescens* Brandeg. Zöe **5:** 162. 1903, non *Ambrosia arborescens* Mill. 1768. Type: Mexico, Baja California, Ascension, *T. S. Brandegee*, April 18, 1889 (UC, no. 88767, not seen; type photograph, NY!). NOTE: Specimens commonly identified with this name.

*Franseria carduacea* Greene, Leaflets Bot. Obs. Crit. **2:** 156. 1912. Type: Mexico, Lower California, Aquaje de Santana, 35 miles N. of San Ignacio, alt. 3400 ft., *E. W. Nelson & E. A. Goldman 7187*, October 4, 1905 (US! no. 565273; photograph, NY!).

*Franseria sanctae-gertrudis* Rydb. N. Am. Fl. **33:** 35. 1922. Type: Mexico, Baja California, rocky slopes, Santa Gertrudis, alt. 6–700 ft., *C. A. Purpus 116*, January–March, 1898 (US! no. 383387; photograph, NY!).

*Franseria acerifolia* M. E. Jones, Contrib. West. Bot. **18:** 78. 1935. Syntypes: Mexico, Lower California, Arroyo Undo Ranch, Loreto, *Marcus E. Jones 27764*, October 26, 1930 (NY!); Cayuca Ranch, Loreto, *M. E. Jones 27765*, October 23, 1930 (US! no. 1589558).

Erect shrub to 30 dm. high or higher. Leaves alternate, petiolate, petioles to 3 cm. long, without obvious decurrent laminar tissue. Lamina ovate-lanceolate to lanceolate in outline, nearly unlobed to pinnately lobed, leaf segments broad, marginal teeth often forming weak secondary lobes; upper surface green, strigose to hispid-scabrous, lower surface lighter, to densely tomentose. Inflorescence racemose-paniculate. Staminate involucre stalked, stalks to 10 mm., the lower often bearing more than one head, involucre to 5 mm. broad, 5–9-lobed, lobes with darkened veins on upper surface but rarely with obvious striations, sinuses separating lobes extending halfway or more to point of stalk attachment. Fruiting involucres 6–10 mm. long, 3–5 mm. wide, 2-flowered; spines 6–12, somewhat flattened, usually uncinate, less than 3 mm. long, scattered over surface of body. Chromosome number unknown.

Flowering: December to March, possibly throughout year.

Range: Central to southern Baja California, Mexico.

Notes: A species with considerable leaf variation, the synonymous taxa being distinguished primarily on this basis. Another complex requiring further study.

10. **Ambrosia chamissonis** (Less.) Greene, Man. Bot. Reg. San Francisco Bay 188. 1894. PLATE V

*Franseria chamissonis* Less. Linnaea **6**: 507. 1831. Type: California, *Cel. de Chamisso* (probably in LE, not seen). NOTE: Plants so named by Lessing were collected on a Russian expedition ("Expeditione Romanzoffiana") to California in the 1820's. Although I have not seen the types, Lessing's detailed description leaves no question as to the identity of the plants included. Among the plants collected by Chamisso, Lessing recognized two varieties, var. *malvaefolia* and var. *bipinnatisecta*, characterized respectively by unlobed and bipinnately lobed leaves (one specimen was noted to have leaves of *malvaefolia* below and *bipinnatisecta* above). Much of the nomenclatural confusion, indicated by the numerous synonyms which follow, has resulted from attempts to distinguish these and other leaf forms within the complex.

*Franseria bipinnatifida* Nutt. Trans. Am. Phil. Soc. ser. 2. **7**: 344. 1840. Type: California, *Nuttall*, in 1835 (?) labeled with an unpublished name (PH!). It is possible that this is an isotype and that the holotype is at BM. NOTE: A sheet labeled "*Franseria bipinnatifida* Nutt." from the Nuttall collections in PH bears three specimens. Two of these, *C. G. Pringle*, April 27, 1882, and *E. Palmer 40*, 1875 (see synonymy of *A. camphorata*) were collected after Nuttall's death and could not have figured in his concept. The third is labeled, by Nuttall, with an unpublished name indicating the decumbent habit. However, it may be that this specimen was at hand when Nuttall described *F. bipinnatifida*, as the description states (loc. cit.): "perennial, herbaceous, decumbent and diffusely branched." Nuttall then equated the species with *F. chamissonis β bipinnatisecta* Less., and described the habit (which is unusual in this species) and morphological features in such a way as to leave no doubt that he was, in fact, dealing with the bipinnatisect form of *A. chamissonis* as recognized here, and that he had seen and examined it in the field, along the Pacific Coast of California.

*Franseria cuneifolia* Nutt. *Ibid.* 345. Type: Oregon (?), Columbia estuary, *Nuttall*, in 1835 (?) (possibly in BM [not seen] or PH!).

*Franseria chamissonis* var. *cuneifolia* (Nutt.) Torr. & Gray, Fl. N. Am. **2**: 293. 1842.

*Franseria lessingii* Meyen & Walp. ex Meyen, Nov. Act. Acad. Caes. Leopold. Carol. **19** (suppl. 1, Nat. Cur., Obs. Bot.): 267. 1843. Type: This is a newly proposed name for the bipinnatifid form of *F. chamissonis*, possibly based upon isotypic material for var. *bipinnatisectis* in the herbarium at Berlin, examined by Meyen and Walpers.

*Gaertnera chamissonis* (Less.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

*Ambrosia bipinnatifida* (Nutt.) Greene, Man. Bot. Reg. San Francisco Bay 187. 1894.

*Franseria bipinnatifida* var. *dubia* Eastw. Proc. Cal. Acad. ser. 3. **1**: 117. 1898. Type: California, Ventura County, San Nicolas Island, *Mrs. Blanche Trask*, April, 1897 (CAS, not seen). NOTE: Although I have not seen this specimen, the type material has been verified by Dr. Elizabeth McClintock. Material from the same collector and locality serves to typify the following synonym.

*Franseria chamissonis* var. *viscida* Eastw. *Ibid.* Type: See preceding note.

*Gaertneria bipinnatifida dubia* (Eastw.) Heller, Muhlenbergia **1**: 6. 1900.

*Gaertneria chamissonis viscida* (Eastw.) Heller, *ibid.*

*Franseria bipinnatifida* var. *insularis* Reiche, Anal. Univ. Chile **112**: 131. 1903. Type: Chile, Isla de la Mocha, en la playa del NE, *Karl Reiche*, in 1892. I have not located this type. NOTE: Distinguished from typical *F. bipinnatifida* Nutt., according to Reiche, principally on the basis of pubescence differences. Reiche notes that the plant is "*probablemente introducida*."

*Franseria bipinnatifida villosa* Eastw. ex Rydb. N. Am. Fl. **33**: 26. 1922, *in synon.*

*Franseria villosa* (Eastw.) Rydb. *Ibid.* Type: California, Mendocino County, near Mendocino, *H. E. Brown 843*, June, 1898 (NY! isotype, US! no. 343666).

*Franseria chamissonis* subsp. *typica* Wigg. & Stockw. Madroño **4**: 120. 1937. Type: Based on *F. chamissonis* var. *malvaefolia* Less.

*Franseria chamissonis* subsp. *bipinnatisecta* Wigg. & Stockw. *Ibid.* Type: Based on *F. chamissonis* var. *bipinnatisecta* Less.

Erect, decumbent or trailing subshrub, becoming very large since stems and leaves trap sand and continue growth by emergent branch tips. Leaves alternate, petiolate, petioles to 8 cm. long, usually shorter, laminar tissue decurrent to base. Lamina broadly ovate to lanceolate in outline, lobing extremely variable, from unlobed to tripinnately lobed; both surfaces gray-green, silky canescent. Inflorescence racemose. Staminate involucres stalked, stalks to 5 mm. long; involucre 3–8 mm. broad, 7–15-lobed, the sinuses shallow, upper surface of lobes often marked with black striations along veins. Fruiting involucres clustered in often heavy masses below staminate racemes, 6–12 mm. long and 3–9 mm. broad; spines 9–20, to 3 mm. long, terete or flattened above, strongly emergent, sharply pointed, scattered over involucre surface. Haploid chromosome number, $n = 18$.

Flowering: Throughout year.

Range: Along Pacific coast of North America from Vancouver Island, British Columbia to Baja California, Mexico. Adventive along South American coast.

Notes: The variability of this species, especially in regard to leaf morphology, has led to considerable taxonomic confusion, as is evident from the synonymy. The basic problem is that two very different leaf forms are found, one unlobed and one pinnately dissected. As Eastwood (op. cit., p. 117) remarked concerning these, "They are most puzzling to the systematist who endeavors to make boundary lines, because they not only appear to run into each other but each is variable even in regard to what are supposed to be its own individual characteristics. Especially this is true as regards foliage, pubescence and size of the heads." Within what must be considered "normal" populations in every locality in which the species exists in abundance, one encounters both extremes as well as all intermediate forms. I have raised self-pollination progeny of the extremes and of intermediates in the greenhouse and it appears that any form is capable of giving rise to any other form. At the same time, however, there may be regional tendencies which need further investigation. Certainly the forces acting to maintain the observed variability, within what must be regarded as a stable and specialized site preference, are very subtle indeed.

11. **Ambrosia chenopodiifolia** (Benth.) Payne, comb. nov. PLATE IV

*Franseria chenopodiifolia* Benth. in Hinds, Bot. Voy. Sulphur 26. 1844. Type: Mexico, Baja California, Bay of Magdalena, *Barclay* (K, not seen; photograph, GH).

*Gaertneria chenopodifolia* Abrams, Bull. N.Y. Bot. Gard. **6:** 461. 1910.

*Franseria lancifolia* Rydb. N. Am. Fl. **33:** 36. 1922. Type: Mexico, Baja California, Cedros Island, *A. W. Anthony 290*, March–June, 1897, (US! no. 313846; photograph, NY!).

Erect shrub, becoming much branched at base, to 35 dm. high. Leaves alternate, petiolate, petioles to 6 cm. long, laminar tissue decurrent to base. Lamina ovate-lanceolate to broadly ovate in outline, to 10 cm. long and 3-nerved, tending to become trilobed, lobes weak, sinuses shallow, rarely somewhat pinnately lobed; both surfaces glandular and pubescent, upper gray-green, tomentose, lower becoming white-tomentose. Inflorescence racemose-spicate, becoming paniculate. Staminate involucre stalked, stalks to 8 mm. long, occasionally with more than one head borne on lower stalks; involucre to 6 mm. broad, 5–10-lobed, sinuses between lobes shallow and often irregular, lobes occasionally marked with brownish to black striations on upper surface. Fruiting involucres clustered on lower inflorescence branches, to 7 mm. long and broad, 2–3-fruited, the body usually thickly clothed with woolly white tomentum from which spines and beaks emerge; spines 12–25, slender, uncinate, to 3 mm. long, scattered over surface of involucre. Haploid chromosome number, $n = 36$.

Flowering: January to June.

Range: Baja California, Mexico, from Comondu north into San Diego Co., California.

Notes: This species is very similar in aspect, habit, and leaf morphology to *A. deltoidea,* a species with which it undoubtedly has close affinity. Ordinarily the two can be distinguished at least on the basis of the characters of the fruiting involucre. *A. chenopodiifolia* is characterized by woolly tomentose involucre bodies with terete, uncinate spines and *A. deltoidea* is characterized by non-woolly involucres with flattened, straight spines (see PLATE IV). However, intermediate specimens with woolly involucre bodies and straight spines or with uncinate spines and non-woolly bodies are frequent. This complex needs further study.

12. **Ambrosia confertiflora** DC. Prodr. **5:** 526. 1836. Type: Mexico, Matamoros, *Berlandier 2297*, October, 1830 (G, not seen; photograph from Hb. Delessert, series 33702, GH, MICH!). PLATE V

*Ambrosia fruticosa* DC. *Ibid.* 525, non *Ambrosia fruticosa* Medic. 1775, nec *Xanthium fruticosum* L.f. 1781, nec *Franseria fruticosa* Phil. 1891. Type: Mexico, Tamaulipas, circa Reynosa, *Berlandier 2112*, April, 1830 (G, not seen; photograph from Hb. Delessert, series 33700, GH, MICH!; isotypes, NY!, GH!).

*Franseria tenuifolia* Harv. & Gray in Gray, Pl. Fendl. in Mem. Am. Acad. ser. 2. **4:** 80. 1849, non *Ambrosia tenuifolia* Spreng. 1826. Type: California,

Poñi Creek, between Bent's Fort and Sante Fé, *Fendler 406* (not seen). NOTE: Although I have been unable to locate this type, the original description applies to *A. confertiflora* as defined here. Also, see discussion for *F. tenuifolia* var. *tripinnatifida* below.

*Franseria tenuifolia* var. *tripinnatifida* Gray, Pl. Lindheim. 2. *in* Boston Jour. Nat. Hist. **6:** 227. 1850. Type: Texas, Mountain prairies of the Liano [Llano], *Lindheimer 640* (not seen). NOTE: I have been unable to locate this type, but the description fits *A. confertiflora*, and a specimen labeled *F. tenuifolia* var. *tripinnatifida* by Gray (New Mexico, *C. Wright 1210*, 1851. NY!) is *A. confertiflora*. Also, isotypes of *A. fruticosa* DC. (*Berlandier 2112*, GH!, NY!) have been annotated by Gray, leaving little question as to the identity of this taxon.

*Xanthidium tenuifolium* Delp. Studi. Lign. Anem. Comp. Artem. 17. 1871. Type: Based upon *Franseria tenuifolia* Harv. & Gray.

*Gaertnera tenuifolia* (Gray) Kuntze. Rev. Gen. Pl. **1:** 339. 1891.

*Franseria confertiflora* (DC.) Rydb. N. Am. Fl. **33:** 28. 1922.

*Franseria caudata* Rydb. *Ibid.* 29. Type: New Mexico, Lincoln County, Gray, *Josephine Skehan 108*, September 1, 1898 (NY!; isotypes, NY!, US!).

*Franseria hispidissima* Rydb. *Ibid.* Type: Mexico, Zacatecas, Real de Pinos, *Leon Diquet* (NY!).

*Franseria incana* Rydb. *Ibid.* 30. Type: Arizona, Ft. Huachuca, *Dr. T. E. Wilcox*, Sept. 1892 (NY!; isotype, NY!).

*Franseria strigulosa* Rydb. *Ibid.* 28. Type: California, Los Angeles County, *L. T. Chamberlain*, Sept. (NY!).

*Franseria pringlei* Rydb. *Ibid.* Type: Mexico, Coahuila, Valley Jimulco, *C. G. Pringle 192*, May 17, 1885 (NY!; isotype, US!).

*Ambrosia simulans* Shinners, Field Lab. **17:** 173. 1949. Type: A new name assigned to *F. tenuifolia* Harv. & Gray because of existence of earlier homonym, *Ambrosia tenuifolia* Spreng.

*Ambrosia caudata* (Rydb.) Shinners, *ibid.* 174.

Erect, perennial herb, perennating from base of stem or by means of adventitious shoots from roots, tending to form large clones; to 18 dm. high. Leaves alternate, petiolate, petioles to 15 cm. long; laminar tissue decurrent, usually with one or more pairs of small lobes below the main laminar region. Lamina ovate-lanceolate to lanceolate in outline, pinnately to tetrapinnately lobed, the lobes lanceolate to linear, attenuated or abruptly terminated, blade to 16 cm. long and 15 cm. broad, usually smaller; both surfaces green to somewhat gray-green, glabrous or nearly so to densely strigose, becoming velutinous. Inflorescence racemose-spicate, often much branched. Staminate involucres stalked, stalks to 8 mm. long, involucre to 10 mm. broad, 5–9-lobed (or more), the lobes obscure and poorly defined or well defined with sinuses extending nearly halfway to point of stalk attachment. Fruiting involucres in sessile, frequently massive clusters below staminate racemes, to 5 mm. long and 4 mm. broad, often much smaller, the base tending to be elongate, leaving the spines arranged on the upper 2/3 of the body, 1 (rarely 2)-flowered; spines 0–20, often fewer than 10, short, 1 mm. or less long to 2 mm. long and slender, uncinate. Haploid chromosome numbers, $n = 36, 54$.

Flowering: Throughout year in various portions of range.

Range: Southwestern United States from Texas and Colorado to California, throughout central Mexico from Nuevo Leon and Tamaulipas through Guanajuato and Jalisco to Sinaloa and Sonora. Adventive in Hawaii on the islands of Oahu and Molokai, and in Puerto Rico.

Notes: An extremely variable species, without doubt the most complex and difficult of the ragweeds, possibly an aggregate species as defined here, needing considerable further study before useful subgroups can be recognized.

13. **Ambrosia cordifolia** (Gray) Payne, comb. nov. PLATE VI

*Franseria cordifolia* Gray, Syn. Fl. N. Am. **1**: 445. 1884. Type: Arizona, Sierra Tucson, *C. G. Pringle*, April 26, 1884 (GH!; isotypes, NY!, US!, MICH!).
*Gaertnera cordifolia* (Gray) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.
*Franseria malvacea* Rydb. N. Am. Fl. **33**: 34. 1922. Type: Mexico, Sinaloa, Culiacan, *Dr. Edward Palmer 1770*, October 25 to November 18, 1891 (NY!; isotype, US!).

Erect shrub, becoming much branched at base, to 13 dm. high. Leaves alternate, petiolate, petioles to 4.5 cm. long, laminar tissue very narrowly decurrent, rarely with a few minute lobes below blade. Lamina ovate-cordate to broadly lanceolate in outline, to 13 cm. long and 10 cm. broad, usually smaller, margin dentate-serrate, 3-veined, weakly trilobed becoming obscurely pinnately lobed, base cordate to cuneate; both surfaces green, upper puberulous, lower lighter, tomentose. Inflorescence racemose-spicate, becoming paniculate. Staminate involucre stalked to subsessile, stalks to 4 mm. long; involucre to 7 mm. broad, shallowly 5–10-lobed, lobes without obvious striations. Fruiting involucres clustered on branches below staminate spikes, to 9 mm. long and 6 mm. broad, 2-fruited; spines 6–30, to 3 mm. long, scattered below the usually divergent beaks, sometimes swollen below, slender above, uncinate. Chromosome number unknown.

Flowering: November to May.

Range: Southern Arizona, south and west into San Luis Potosi, Sonora, Sinaloa, and Baja California, Mexico.

14. **Ambrosia deltoidea** (Torr.) Payne, comb. nov. PLATE IV

*Franseria deltoidea* Torr. Pl. Fremont. in Smithson. Contr. Knowl. **6**: 15. 1854. Type: Southern California, on the Gila River, Fremont in 1849 (NY!). (Label includes pencil drawings of floral structures — Torrey's?). Sheet bears two specimens in addition to the type (which is at the extreme left): *Schott V. 855* (central) and *C. C. Parry 549* (extreme right). The latter is a paratype (duplicate of paratype, NY!).
*Gaertnera deltodea* (Torr.) Kuntze, Rev. Gen. Pl. **1**: 339. 1891.

Erect shrub, to 5 dm. high, occasionally higher, usually much branched from base. Leaves alternate, petiolate, petiole to 2 cm. long, occasionally longer, laminar tissue narrowly decurrent to stem. Lamina narrowly lanceolate to deltoid-lanceolate or somewhat rhombic, abruptly expanded

from cuneate (to nearly straight) base, margin serrate or doubly serrate, unlobed or occasionally with few weak lobes; both surfaces gray-green to whitish-tomentose, strongly resinous and sticky. Inflorescence spicate-racemose to paniculate. Staminate involucre stalked to subsessile, stalks to 5 mm. long; involucres to 7 mm. broad, 6–9(–13)-lobed, lobes sometimes weakly defined, sinuses separating lobes usually extending less than halfway to point of stalk attachment, obscurely striated on upper surface or without striations. Fruiting involucres clustered on axis below staminate spike or on lateral branches, involucres to 10 mm. long and 12 mm. broad, 2 (rarely more)-flowered; spines to 18 (occasionally more), often the lowermost in a well defined whorl resembling the phyllaries of less specialized involucres, flattened, very sharply pointed, rarely somewhat uncinate, to 5 mm. long. Haploid chromosome number, $n = 18$.

Flowering: February to July.

Range: Southern Arizona, extending into Sonora and Baja California, Mexico.

Notes: A species similar to, and with intermediate forms resembling, *A. chenopodiifolia* (see notes for *A. chenopodiifolia*).

15. **Ambrosia divaricata** (Brandeg.) Payne, Pap. Mich. Acad. **49**: 44. 1964.

*Franseria divaricata* Brandeg. Proc. Calif. Acad. ser. 2. **2**: 171. 1889. Type: Mexico, Lower California, San Gregorio, *T. S. Brandegee*, Feb. 6, 1889 (UC, no. 88805, not seen; photograph, NY!; isotype, US!, no. 47803).

Erect, much branched shrub, probably more than 3 dm. high. Leaves alternate, petiolate, petioles to 15 mm. long, laminar tissue decurrent to base, occasionally with one or more pairs of minute lobes below main laminar region. Lamina broadly ovate, to 4 cm. long and 3.5 cm. broad, 3-veined, shallowly 3–7-lobed, the lobes broad; green both surfaces, somewhat lighter to gray-green below, strigose, becoming tomentose. Inflorescence racemose-paniculate, the lower staminate stalks often bearing more than one head. Staminate heads stalked, stalks to 2 cm. long (or longer); involucres to 7 mm. broad, 7–11-lobed, the lobes well defined, upper surfaces sometimes with weak striations. Fruiting involucres clustered on stalks below staminate racemes, to 9 mm. long and broad, 2-flowered; spines to more than 30, scattered, slender, uncinate, to 3 mm. long. Chromosome number unknown.

Flowering: January to April.

Range: Central Baja California, Mexico.

Notes: A species of great similarity to *A. magdalenae*, being distinguished primarily by the differences in leaf morphology.

16. **Ambrosia dumosa** (Gray) Payne, comb. nov. PLATE VI

*Franseria dumosa* Gray in Torr. & Frem. in Fremont, Rept. Expl. Exped. Rocky Mtns. 316. 1845. Type: California, sandy uplands of the Mohave River, very common in all that region of California, *Fremont 374*, 1844 (NY!).

*Franseria albicaulis* Torr. Pl. Frem. in Smithson. Contr. Knowl. **6:** 16. 1853. Type: California, Fremont's Expedition, *Fremont*, 1849 (NY!).
*Franseria dumosa* var. *albicaulis* (Torr.) Gray in Torrey, Bot. Mex. Bound. Surv. 87. 1859.
*Gaertnera dumosa* (Gray) Kuntze, Rev. Gen. Pl. **1:** 339. 1891.

Erect, much branched shrub, to 9 dm. high. Leaves alternate, petiolate, petioles to 20 mm. long, usually much shorter, laminar tissue narrowly decurrent to base. Lamina broadly ovate to narrowly elliptic-lanceolate, to 40 mm. long and 30 mm. broad, usually much smaller, pinnately to bi- or tripinnately lobed, lobes linear to distally expanded; both surfaces gray-green, puberulous, becoming white-tomentose on the under surface. Inflorescence racemose-paniculate, all stalks usually bearing distal staminate heads and one or more proximal pistillate heads subtended by small bracts; capitulous stalks to 8 mm. long. Staminate involucre 3–7 mm. broad, 5–9-lobed, sinuses separating lobes extending about halfway to point of stalk attachment, lobes without striations. Fruiting involucres to 9 mm. long and broad, 1- or 2-fruited; spines 12–30, scattered over surface of involucre, flattened, straight. Haploid chromosome number, $n = 18, 36, 54, 63$ (72?).

Flowering: February to July (fruiting specimens have been collected into September).

Range: Arid regions of Utah, Arizona, Nevada and California, south into Sonora and Baja California, Mexico.

Notes: The organization of the inflorescence of this species is unique for *Ambrosia*. Also, it is the only species which spans all ploidal levels known for the genus, from diploid to octoploid. Several variants may be recognized in the field, and the species may be of greater complexity than is indicated here.

### 17. **Ambrosia eriocentra** (Gray) Payne, comb. nov. PLATE VI

*Franseria eriocentra* Gray, Proc. Am. Acad. **7:** 355. 1868. Type: Arizona, East slope of Providence Mountain, *J. G. Cooper*, May, 1861 (GH!).
*Gaertnera eriocentra* (Gray) Kuntze, Rev. Gen. Pl. **1:** 339. 1891.

Erect, much branched shrub, to 18 dm. high. Leaves alternate, petiolate to subsessile, petioles to 3 mm. long. Lamina elliptical or narrowly lanceolate to deltoid-lanceolate in outline, to 90 mm. long and 30 mm. broad, usually smaller, unlobed to marginally pinnately lobed, the rachis lamina usually comprising largest portion of blade; upper surface green, puberulous to tomentose, main veins frequently whitened by pubescence, under surface becoming white woolly-tomentose; margin usually strongly revolute. Inflorescence spicate, becoming racemose. Staminate involucre subsessile to stalked, stalks to 2 mm. long, lower stalks often with two or more closely approximate heads resembling a single large head; involucres to 7 mm. broad, 5–9-lobed, the sinuses between lobes shallow to more than halfway to point of stalk attachment, without obvious striations on upper surface. Fruiting involucres to 10 mm. long and 11 mm. broad, 1(–2?)-

flowered; spines to 20, usually emerging near equator of fruit body, flat, sharply pointed, more or less covered with long, white, silky hairs. Haploid chromosome number, $n = 18$.

Flowering: April to July.

Range: Southern Arizona, scattered in arid regions of Nevada, Utah, and California.

18. **Ambrosia flexuosa** (Gray) Payne, comb. nov.

*Franseria flexuosa* Gray, Proc. Am. Acad. ser. 2. **12** (whole series 20): 298. 1885. Type: Mexico, Lower California, *H. C. & C. R. Orcutt 1103*, July 8, 1884 (GH!; type photograph, NY!).

Erect shrub, similar in general aspect to *A. carduacea*. Leaves alternate, petiolate, petioles to 1 cm. long. Lamina narrowly lanceolate to deltoid-lanceolate in outline, to 5 cm. long and 3 cm. broad, cuneate at base, unlobed to weakly pinnately lobed by prolongation of marginal teeth, teeth stiff; both surfaces green, under surface somewhat woolly before maturity, veins prominent on under surface, yellowish. Inflorescence racemose-paniculate. Staminate involucres stalked, stalks to 7 mm. long; involucres to 5 mm. broad, 5–10-lobed, lobes marked on the upper surface with dark striations. Fruiting involucres in clusters on short or long stalks below staminate racemes, to 8 mm. long and 6 mm. broad, 2-flowered; spines to 15 (or more?), terete, uncinate, broadened at base. Chromosome number unknown.

Flowering: July.

Range: Baja California, Mexico, known only from type collection.

Notes: A species of questionable nature because of the limited material. Gray noted that the foliage was somewhat intermediate in character between *A. ambrosioides* and *A. ilicifolia*, but the fruiting involucres are very different from both, more closely resembling those of *A. cordifolia*. The abundance with which fruiting involucres have been matured on this specimen would argue against a hybrid nature.

19. **Ambrosia grayi** (Nels.) Shinners, Field Lab. 17: 174. 1949.

*Franseria tomentosa* Gray, Pl. Fendl. in Mem. Am. Acad. ser. 2. **4**: 80. 1849, non *A. tomentosa* Nutt. 1818, nec *Gaertneria tomentosa* (Nutt.) Nels. 1909. Type: Kansas (?), high banks of Walnut Creek, between Council Grove and Fort Mann, of the Arkansas River, *Fendler 412* (GH, not seen).

*Gaertnera tomentosa* (Gray) Kuntze, Rev. Gen. Pl. 1: 339. 1891.

*Gaertneria grayi* Nels. Bot. Gaz. **34:** 35. 1902. NOTE: Based upon *Franseria tomentosa* Gray. New name proposed by Nelson because of earlier homonym, *Gaertneria tomentosa* Nels. (= *A. tomentosa* Nutt.).

*Franseria grayi* (Nels.) Nels. New Man. Bot. Centr. Rocky Mtns. 542. 1909.

Upright, perennial herb, perennating by means of adventitious shoots from the roots, forming large clonal populations. Leaves alternate, petiolate, petioles to 5 cm. long, laminar tissue decurrent to base, with several small lobes below main laminar region. Lamina ovate-deltoid to lanceolate in

outline, to 10 cm. long and 8 cm. wide, irregularly pinnately lobed, major basal lobes and terminal lobe much the largest, large lobes lanceolate-elliptical, serrate, both surfaces (and entire plant) silvery gray-canescent. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 5 mm., involucres to 5 mm. broad, 5–9-lobed; lobes often somewhat irregular, shallow, upper surface with dark striations along midveins obscured by pubescence. Fruiting involucres in small axillary clusters below staminate spikes, to 7 mm. long and 4 mm. broad, 2-flowered; spines to 15, scattered, narrowed to slender uncinate tips. Haploid chromosome number, $n = 18$.

Flowering: July to October.

Range: Low, moist areas throughout Kansas and Nebraska, sporadically in Oklahoma, Colorado, and Texas.

Notes: A species well known under the name *Franseria tomentosa*; one of the more handsome ragweeds by virtue of the silvery pubescence.

20. **Ambrosia ilicifolia** (Gray) Payne, comb. nov. PLATE VII

*Franseria ilicifolia* Gray, Proc. Am. Acad. **11:** 77. 1876. Type: California, Southern part of San Diego County, Tantillas Cañon (GH!).
*Gaertnera ilicifolia* (Gray) Kuntze, Rev. Gen. Pl. **1:** 339. 1891.

Erect or semi-prostrate shrub, to 12 dm. high. Leaves alternate, sessile, clasping the stem. Lamina broadly ovate, to 9 cm. long and 7.5 cm. broad, usually smaller, typically unlobed but with strong, prickly, marginal teeth, the teeth often prolonged into weak lobes; both surfaces gray-green, minutely glandular-punctate, with ciliate hairs on margins and along veins; stiff and coriaceous, veins whitened and prominent on under surface, sticky and with a strongly resinous odor when fresh. Inflorescence racemose. Staminate involucres stalked, stalks to 12 mm.; involucres to 35 mm. broad including the usually prominent attenuate lobes, lobes to 15, without striations. Fruiting involucres in axillary clusters below staminate racemes, nearly globose, to 20 mm. long and broad; spines numerous, to 50 or more, scattered, to 6 mm. long, slender, uncinate. Haploid chromosome number, $n = 18$.

Flowering: February to June.

Range: Desert regions of southern Arizona and California, south into Sonora and Baja California, Mexico.

21. **Ambrosia linearis** (Rydb.) Payne, comb. nov. PLATE VIII

*Gaertneria linearis* Rydb. Bull. Torrey Club **32:** 133. 1905. Type: Colorado, Calhan, *DeAlton Saunders*, July, 1893 (NY!).
*Franseria linearis* (Rydb.) Rydb. N. Am. Fl. **33:** 27. 1922.

Erect, perennial, shrubby herb, perennating by means of adventitious shoots from the base of the stem and from roots. Leaves alternate, sessile. Lamina ovate to lanceolate in outline, to 25 mm. long and 15 mm. broad, pinnately or bipinnately lobed, lobes and rachis more or less linear,

margin revolute; upper surface green, strigose, lower surface white woolly-tomentose. Inflorescence racemose-spicate. Staminate involucres occasionally subtended by bracts, subsessile with stalks to ca. 1 mm., involucres to 5 mm. broad, 5–9-lobed, sinuses separating lobes usually extending less than halfway to point of stalk attachment; lobes without obvious striations. Fruiting involucres borne singly or in small clusters in axils of leaves below staminate spike, ca. 3.5 mm. long and 2.5 mm. broad, 1-flowered; spines to 9, arranged more or less in a single whorl near apex of body, terete, uncinate, to ca. 1 mm. long. Chromosome number unknown.

Flowering: July.

Range: Colorado, Lincoln and El Paso Counties, known only from the type and one other specimen (*Ownbey 1325*) collected in 1937.

Notes: A very distinctive species, inexplicably rarely collected.

22. **Ambrosia magdalenae** (Brandeg.) Payne, comb. nov. PLATE VIII

*Franseria magdalenae* Brandeg. Proc. Calif. Acad. ser. 2. **2:** 170. 1889. Type: Mexico, Lower California, Magdalena Island, *T. S. Brandegee*, Jan. 13, 1889 (UC, no. 88804, not seen; isotype, US! no. 47365).

*Franseria intricata* Rydb. N. Am. Fl. **33:** 33. 1922. Type: Mexico, Lower California, San Bartolome Bay, *J. N. Rose 16196*, March 13, 1911 (NY!; isotype US!, no. 638267).

Erect, much branched shrub, to 2 dm. high. Leaves alternate, petiolate, petioles to 4 cm. long, laminar tissue narrowly decurrent to base. Lamina ovate to ovate-lanceolate in outline, to 5.5 cm. long and 3.5 cm. broad, irregularly bipinnately lobed, often with one or more pairs of minute lobes below the main laminar region; upper surface green, sparingly tomentose, lower similiar, to white woolly-tomentose. Inflorescence racemose to racemose-paniculate. Staminate involucres stalked, stalks to 10 mm. long, the lowermost occasionally bearing more than one head; involucre to 5 mm. broad, lobes to 12, sometimes with weak striations along midvein, sinuses between lobes usually extending less than halfway to point of stalk attachment. Fruiting involucres in axillary clusters or clustered on branches below staminate raceme, subglobose, to 8 mm. long and 11 mm. broad, 2-flowered; spines to more than 30, scattered, slender, uncinate, to 3 mm. long. Chromosome number unknown.

Flowering: January to April.

Range: Central Baja California, Mexico.

Notes: A species with considerable variability, particularly in leaf morphology and pubescence. Closely resembling *A. divaricata*, a taxon distinguished primarily on the basis of leaf differences.

23. **Ambrosia nivea** (Rob. & Fern.) Payne, comb. nov. PLATE VIII

*Franseria nivea* Rob. & Fern. Proc. Am. Acad. **30:** 117. 1895. Type: Mexico, Chihuahua, Plains near Casas Grandes, *C. V. Hartman 813*, 10 Oct. 1891. (GH!; isotypes, NY!, US!, no. 306295).

Erect shrub, to 2.5 dm. high. Leaves alternate, petiolate, petioles to 4 cm. long, laminar tissue decurrent to base, often with 1–3 or more pairs of small lobes below main laminar region. Lamina ovate to triangular in outline, to 80 mm. long and 70 mm. wide or larger, irregularly bi- to tripinnately lobed, both surfaces gray-green, silky-canescent. Inflorescence racemose-spicate. Staminate involucre stalked, stalks to 5 mm. long; involucres to 4 mm. broad, lobes to 10, the distal lobes tending to be somewhat more pronounced, sinuses separating lobes shallow, upper surfaces of lobes without striations. Fruiting involucres clustered in axils of leaves subtending staminate racemes, to 7 mm. long and 6 mm. broad, 2–3-flowered; spines to 20, scattered, to 3 mm. long, terete, heavy, straight. Chromosome number unknown.

Flowering: October.

Range: Northwestern Chihuahua (known only from type collection).

Notes: A distinctive, and unquestionably valid species, even though known only from the type collection.

24. **Ambrosia tomentosa** Nutt. Gen. Am. Pl. 2: 186. 1818., non *Franseria tomentosa* Gray, 1849, nec *Gaertnera tomentosa* (Gray) Kuntze, 1891. Type: In upper Louisiana on the banks of the Missouri, *Nuttall* (probably BM). NOTE: I have been unable to locate this type in Nuttall's herbarium in PH or elsewhere. However, Nuttall's short description leaves no doubt that he was dealing with the taxon described here, viz.: "Perennial; stem low; leaves bipinnatifid, underside white and tomentose; spikes solitary."

*Franseria discolor* Nutt. Trans. Am. Phil. Soc. ser. 2 **7:** 345. 1840. Type: In the Rocky Mountains, near the Colorado of the West, *Nuttall* (PH!).

*Xanthidium discolor* (Nutt.) Delp. Studi Lign. Anem. Comp. Artem. 17. 1871.

*Franseria exigua* Wawra in Beck, It. Princ. S. Cob. **2:** 41. 1888. Type: Nordamerika, In den Prairien, *Wawra I 13.* I have been unable to locate this type. NOTE: Wawra has included a beautiful and detailed illustration with the description (*Taf. 8, Fig. B*, loc. cit.) which leaves no question whatsoever about the identity of this taxon.

*Gaertnera discolor* (Nutt.) Kuntze, Rev. Gen. Pl. **1:** 339. 1891.

*Gaertneria tomentosa* (Nutt.) Nels. Bot. Gaz. **34:** 34. 1902.

*Franseria tomentosa* (Nutt.) Nels. New Man. Bot. Centr. Rocky Mtns. 542. 1909.

Erect or reclining, perennial herb, perennating by means of adventitious shoots from the roots, forming clonal populations. Leaves alternate, petiolate, petioles to 10 cm. long, laminar tissue decurrent to base, usually with several pairs of small lobes below the main laminar area often obscuring the distinction between petiole and lamina. Lamina ovate-lanceolate in outline, to 10 cm. long and 6 cm. broad, irregularly bi- or tripinnately lobed; upper surface dark green, minutely scabrous, lower surface white woolly-tomentose, margins revolute. Inflorescence racemose-spicate. Staminate involucres stalked, stalks to 10 mm.; involucres to 7 mm. broad,

lobes to 12, sinuses separating lobes extending halfway or less to point of stalk attachment; upper surface of lobes with black striations, mostly along the midveins. Fruiting involucres in sessile clusters in axils of leaves subtending staminate racemes, to 6 mm. long and 3.5 mm. broad, 2-flowered; spines 0–10, scattered, ca. 1 mm. long (rarely to 3 mm.), somewhat appressed. Chromosome number unknown.

Flowering: May to August.

Range: Prairie and semi-arid regions of Wyoming, Nebraska, Colorado, New Mexico, and Arizona; sporadic in Idaho, Iowa, and South Dakota.

Notes: Aptly described by Nuttall (as *Franseria discolor*) as "A remarkable and distinct, as well as elegant species," a comment based, no doubt, on the striking appearance of the white under surface of the leaf, rimmed by the dark green, revolute margin.

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## EXPLANATION OF PLATES

Except in FIGS. 38 and 60, staminate and pistillate involucres have been illustrated without pubescence.

### PLATE I

FIGS. 1–5. *Ambrosia acuminata* (all from *Brandegee*, Feb. 11, 1889, US). 1, Inflorescence, × 0.5; 2, staminate head, × 3.3; 3, pale from staminate head, × 10; 4, fruiting involucre, × 3.3; 5, leaf silhouette, × 0.33.

FIGS. 6–10. *Ambrosia ambrosioides*. 6, Inflorescence, × 0.5; 7, staminate head,

× 3.3 (6 & 7, from *Wiggins 6379*, MICH); 8, pale from staminate head, × 10 (from *Peebles & Loomis 6728*, ARIZ); 9, fruiting involucre, × 3.3 (from *Peebles 15041*, ARIZ); 10, leaf silhouette (photoduplicated from greenhouse specimen, *Payne AJL*).

FIGS. 11–14, *Ambrosia artemisioides* (all from *Williams 2527*, NY). 11, Inflorescence, × 0.5; 12, staminate head, × 3.3; 13, fruiting involucres, × 3.3; 14, leaf silhouettes, × 1.

## PLATE II

FIGS. 15–19, *Ambrosia arborescens*. 15, Inflorescence, × 0.5; 16, staminate head, × 3.3; 17, pale from staminate head, × 10 (15, 16 & 17 from *Killip & Smith 17884*, NY); 18, fruiting involucres, × 3.3 (18a from *Killip & Smith 19676*, NY); 18b from *Pennell 2636*, NY); 19, leaf silhouette, × 0.33 (from *Steinbeck 8817*, NY).

FIGS. 20–24, *Ambrosia carduacea*. 20, Inflorescence, × 0.5; 21, staminate head, × 3.3; 22, pale from staminate head, × 10 (20, 21 & 22 from *Shreve 6944*, ARIZ); 23, fruiting involucres, × 3.3 (23a from *Shreve 6944*; 23b from *Gentry 4128*, ARIZ); 24, leaf silhouettes, × 0.33 (24a & b from *Shreve 6944*, ARIZ; 24c from *Rempel 151*, ARIZ).

## PLATE III

FIGS. 25–29, *Ambrosia camphorata*. 25, Inflorescence, × 0.5 (from *Payne 4175*, MICH); 26, staminate heads, × 3.3 (26a from *Payne 4175*, MICH; 26b from *M. E. Jones 24058*, MICH); 27, pale from staminate head, × 10 (from *Payne 4175*, MICH); 28, fruiting involucres, × 3.3 (28a from *Payne 4000*, MICH; 28b from *Payne 4175*, MICH; 28c from *Palmer 757*, NY; 28d from *Palmer 881*, NY; 28e from *Wiggins 7935*, MICH; 28f from *Greene*, April 24, 1885, NY; 28g from *M. E. Jones 24647*, NY; 28h from *Broder 618*, MICH); 29, leaf silhouettes, × 0.33 (29a–g photoduplicated from population sample from southern San Luis Potosi, Mexico, *Payne 4007*, MICH; 29h photoduplicated from greenhouse specimen, *Payne BCK*).

## PLATE IV

FIGS. 30–34, *Ambrosia canescens*. 30, Inflorescence, × 0.5; 31, staminate heads, × 3.3; 32, pale from staminate head, × 10 (30, 31 & 32 from *Payne 4030*, MICH); 33, fruiting involucres, × 3.3 (from a single specimen, *Payne 4049*, MICH); 34, leaf silhouettes, × 0.33 (photoduplicated from population sample from Jalisco, Mexico, *Payne 4121*, MICH).

FIGS. 35–39. *Ambrosia chenopodiifolia*. 35, Inflorescence, × 0.5 (from *M. E. Jones 3702*, NY); 36, staminate head, × 3.3; 37, pale from staminate head (36 & 37 from *Orcutt*, April 10, 1885, NY); 38, fruiting involucres, × 3.3 (38a from *Orcutt*, May 7, 1886, MICH; 38b from *Palmer 731*, NY); 39, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne BDK*).

FIGS. 40–44, *Ambrosia deltoidea*. 40, Inflorescence, × 0.5 (from *Shreve 7506*, ARIZ, and from *Peebles 15038*, ARIZ); 41, staminate head, × 3.3; 42, pale from staminate head, × 10 (41 & 42 from *Benson 10701*, ARIZ); 43, fruiting involucres, × 3.3 (43a from *Peebles 15038*, ARIZ; 43b from *Gillespie 5436*, NY); 44, leaf silhouettes (photoduplicated from greenhouse population, *Payne AJP*).

## PLATE V

FIG. 45, *Ambrosia chamissonis*, leaf silhouettes, × 0.33 (from greenhouse

grown population and progeny from Marin County, California; each leaf represents a different specimen).

FIG. 46, *Ambrosia confertiflora*, leaf silhouettes, × 0.33 (from population in southeastern Coahuila, Mexico, *Payne 3767*, MICH; each leaf represents a different specimen).

## PLATE VI

FIGS. 47–51, *Ambrosia cordifolia*. 47, Inflorescence, × 0.5; 48, staminate heads, × 3.3; 49, pale from staminate head, × 10 (47, 48 & 49 from *Shreve 10016*, MICH); 50, fruiting involucres, × 3.3 (50a from *Thornber*, May 10, 1913, ARIZ; 50b from *Turkham*, April 19, 1942, ARIZ); 51, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne AJH*).

FIGS. 52–56, *Ambrosia dumosa*. 52, Inflorescence, × 0.5 (from *Harrison & Beldon 3577*, ARIZ); 53, capitulous branch with mature staminate and immature pistillate heads, × 3.3; 54, pale from staminate head, × 10 (53 & 54 from greenhouse specimen, *Payne BDG-a*); 55, fruiting involucres, × 3.3; (55a from greenhouse specimen, *Payne BDG-a*; 55b from *Humphrey SCS-767*, ARIZ); 56, leaf silhouettes, × 0.33 (photoduplicated from greenhouse population, *Payne BDG*).

FIGS. 57–61, *Ambrosia eriocentra*. 57, Inflorescence, × 0.5; 58, staminate head, × 3.3; 59, pale from staminate head, × 10 (57, 58 & 59 from *Kearney & Peebles 13161*, NY); 60, fruiting involucre, × 3.3 (from *Wolf 10683*, NY); 61, leaf silhouettes, × 0.33 (photoduplicated from greenhouse specimen, *Payne AJR*).

## PLATE VII

FIGS. 62–67, *Ambrosia ilicifolia*. 62, Inflorescence, × 0.5; 63, staminate head, × 3.3; 64, floret from staminate head, × 10; 65, pale from staminate head, × 10 (62, 63, 64 & 65 from *M. E. Jones*, Feb. 27, 1924, NY); 66, fruiting involucre, × 3.3 (from *Ahles 9087*, ILL); 67, leaf silhouettes, × 0.33 (photoduplicated from greenhouse specimen, *Payne AJO*).

## PLATE VIII

FIGS. 68–72, *Ambrosia linearis*. 68, Inflorescence, × 0.5; 69, staminate heads, × 3.3; 70, pales from staminate head, × 10 (68, 69 & 70 from *Ownbey 1325*, NY); 71, fruiting involucres, × 3.3 (71a from *Saunders*, July, 1893, NY; 71b from *Ownbey 1325*, NY); 72, leaf silhouettes, × 1 (72a & b from *Ownbey 1325*, NY; 72c from *Saunders*, July, 1893, NY).

FIGS. 73–77, *Ambrosia magdalenae* (all from *Brandegee*, Jan. 13, 1889, NY). 73, Inflorescence, × 0.5; 74, staminate head, × 3.3; 75, pale from staminate head, × 10; 76, fruiting involucre, × 3.3; 77, leaf silhouette, × 0.33.

FIGS. 78–82, *Ambrosia nivea* (all from *Hartman 813*, NY). 78, Inflorescence, × 0.5; 79, staminate head, × 3.3; 80, pale from staminate head, × 10; 81, fruiting involucre, × 3.3; 82, leaf silhouette, × 0.33.

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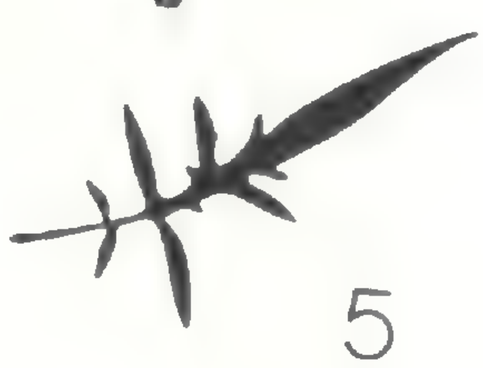
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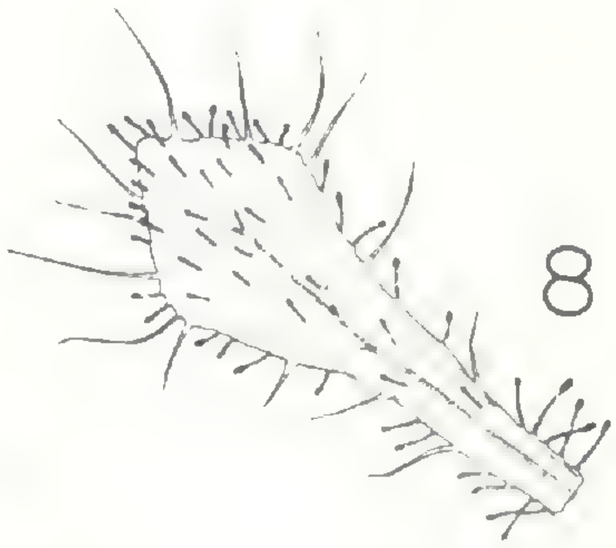
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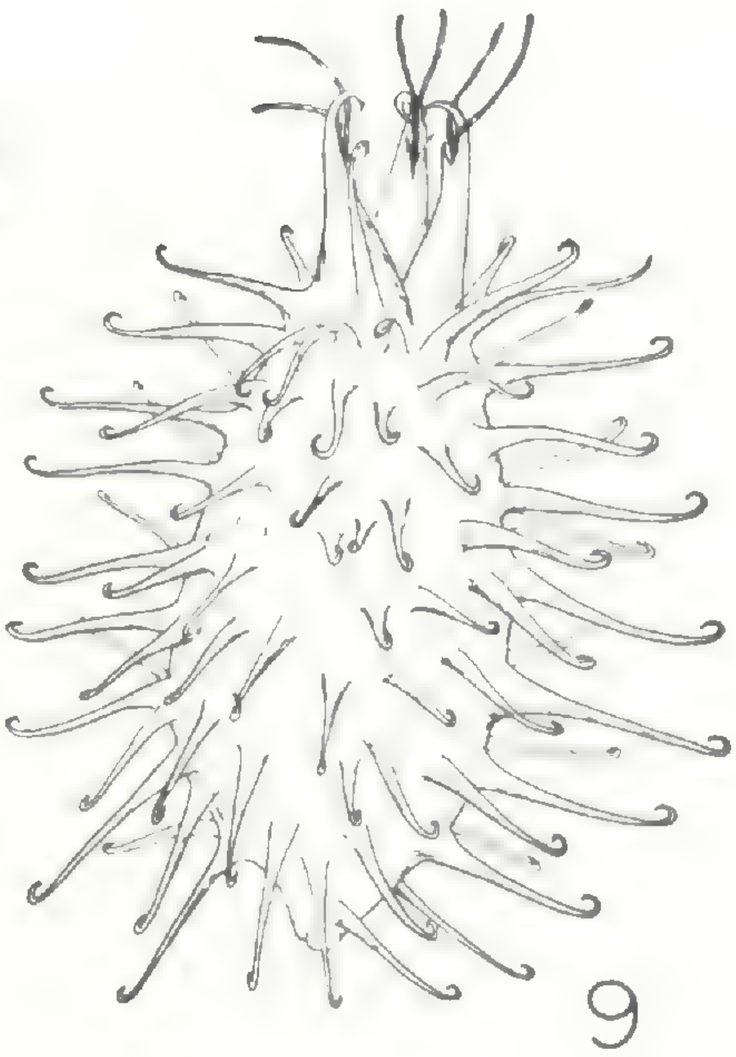
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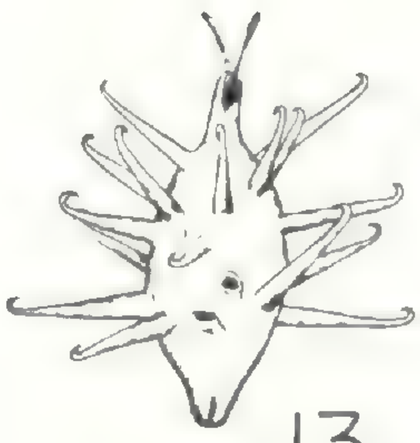
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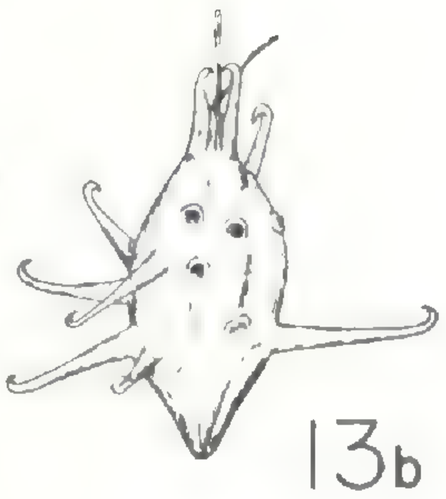
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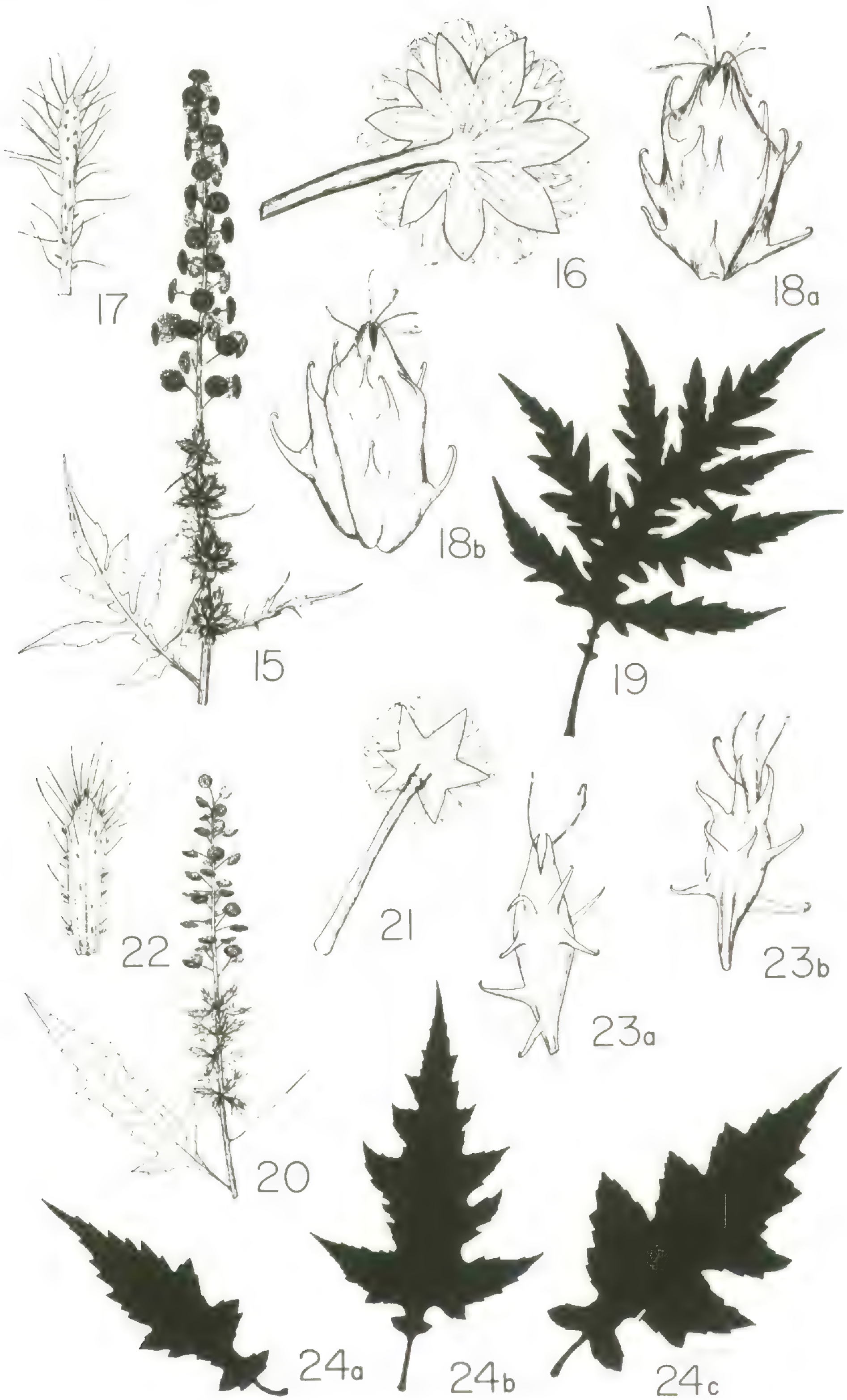


PAYNE, THE GENUS AMBROSIA

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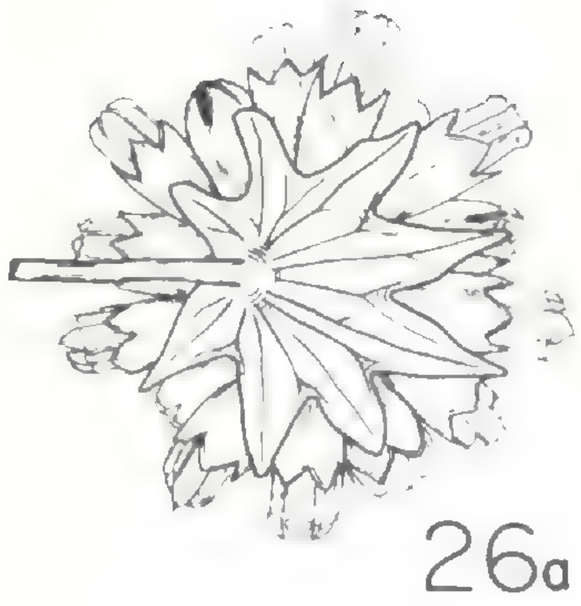
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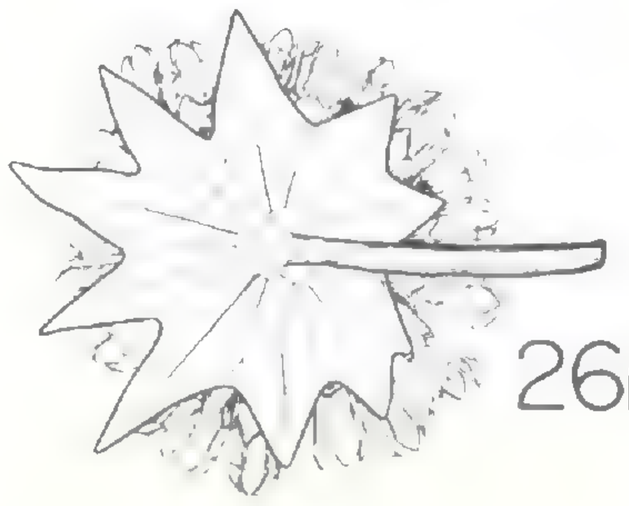
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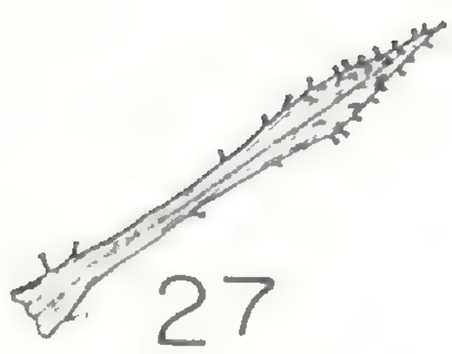
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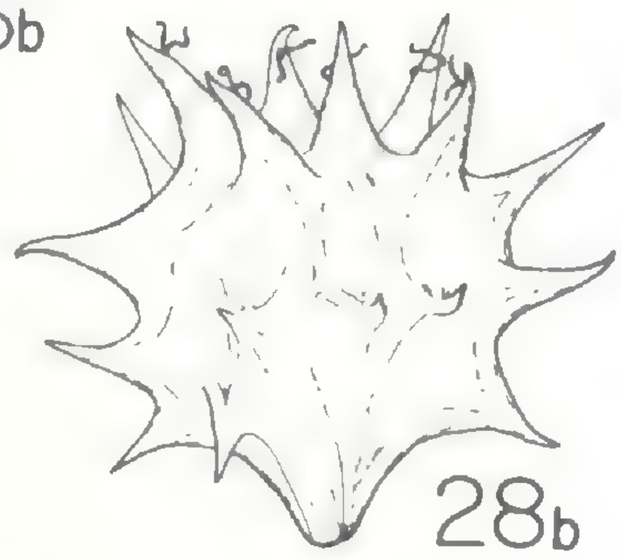
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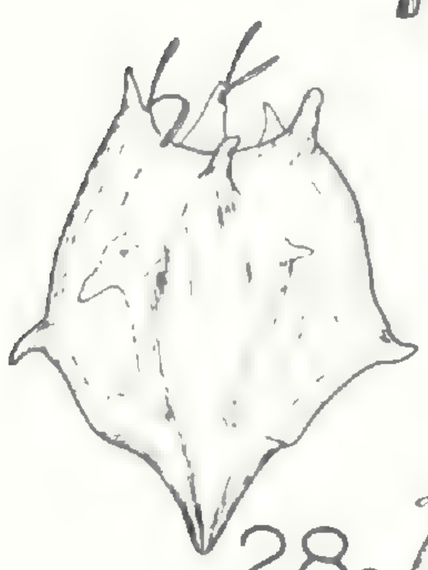
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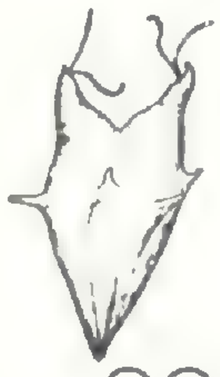
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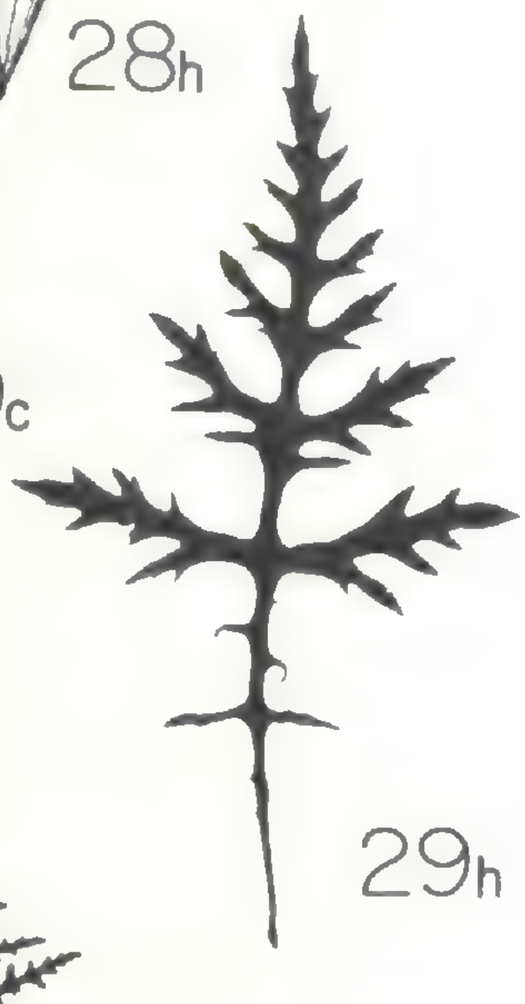
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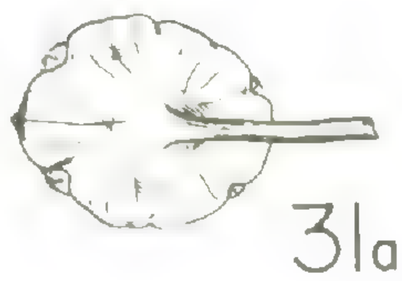
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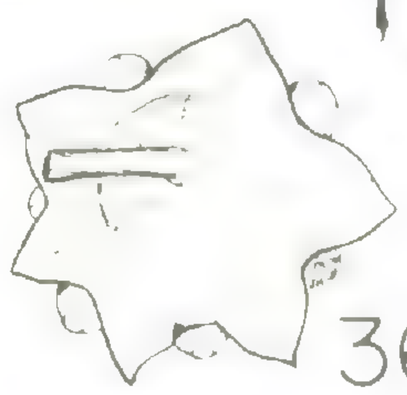
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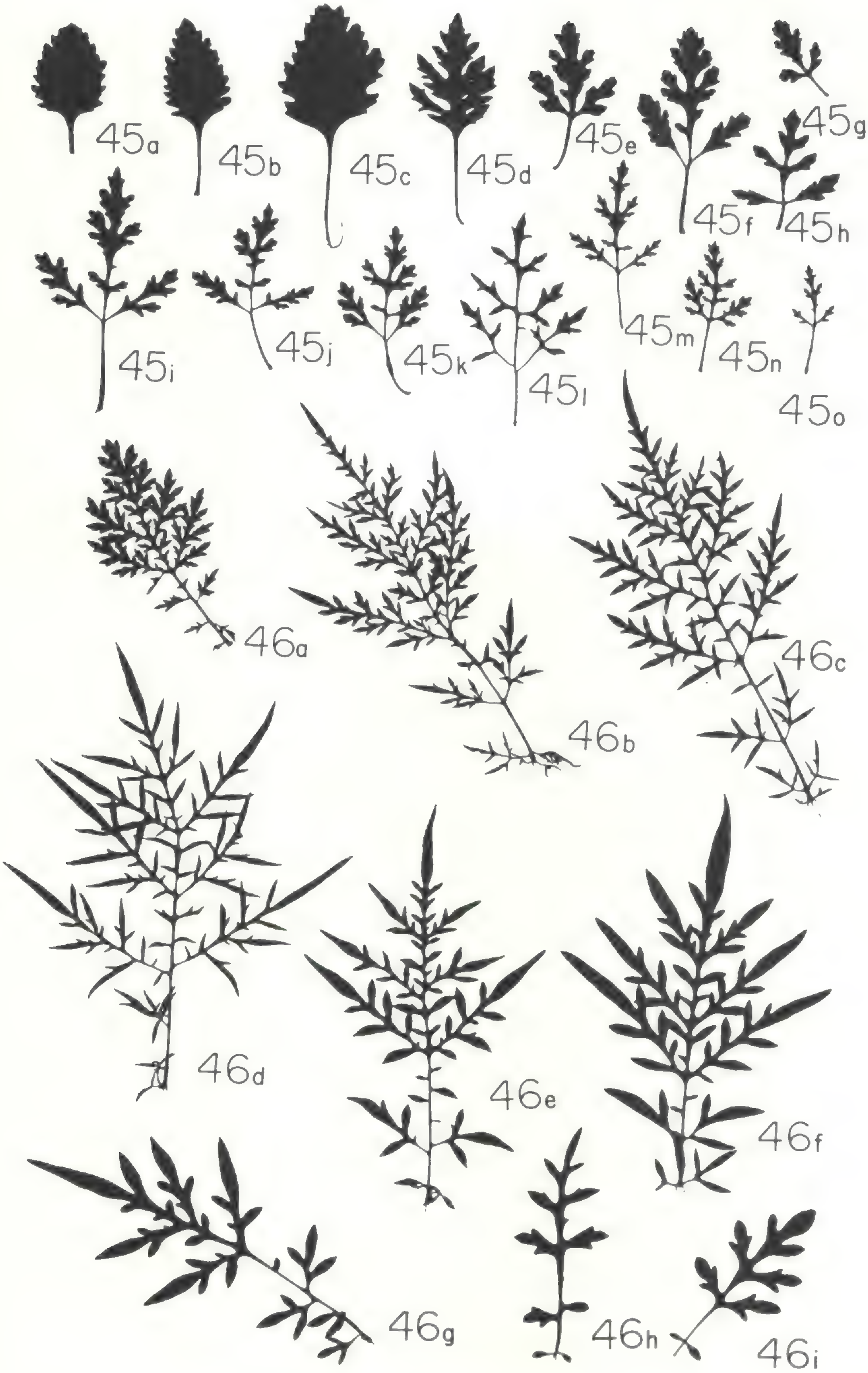


PAYNE, THE GENUS AMBROSIA

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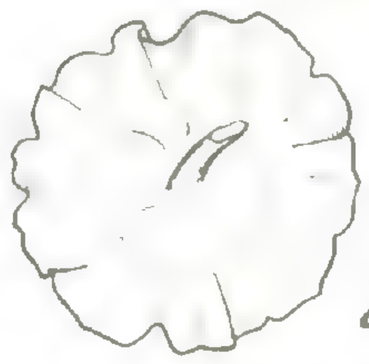

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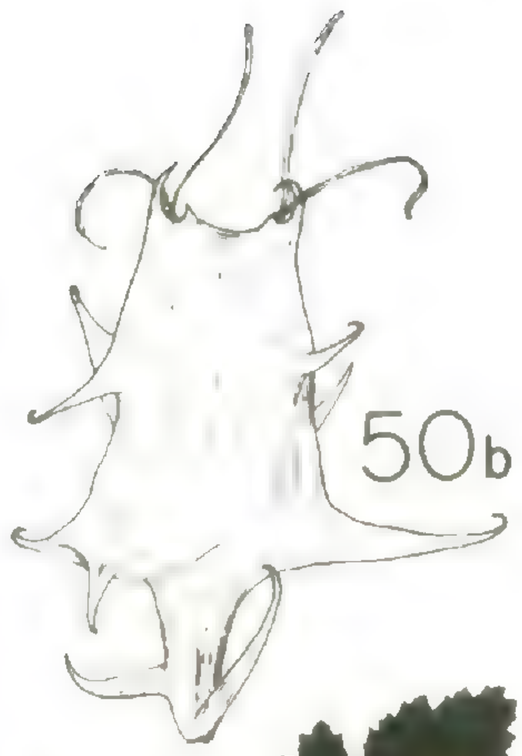

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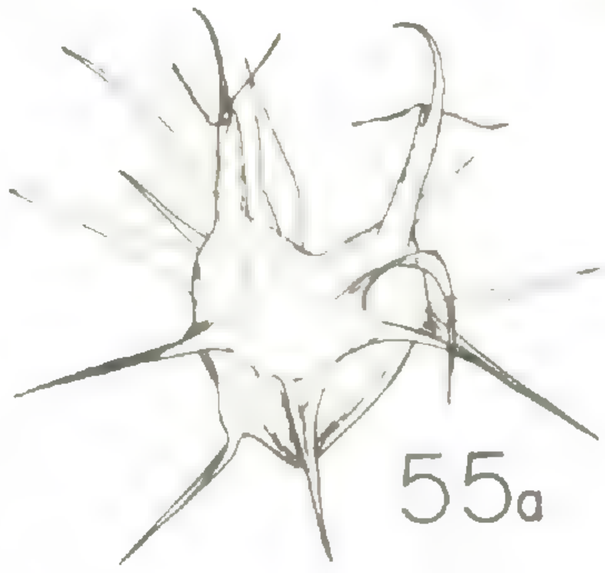

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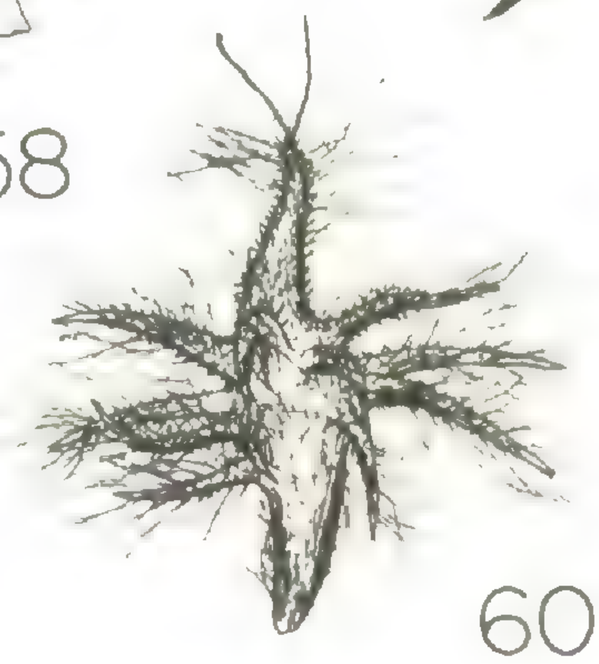

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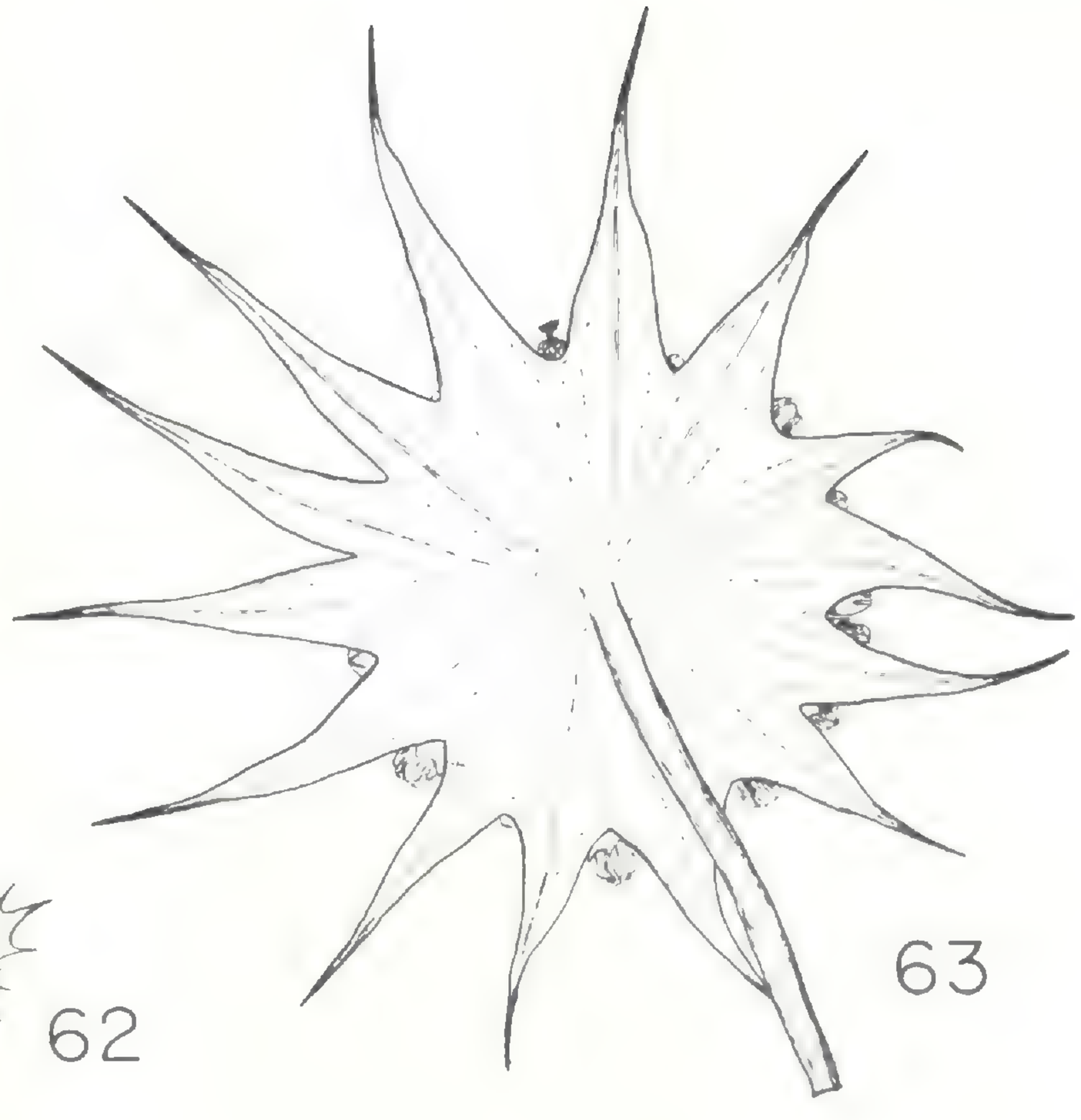

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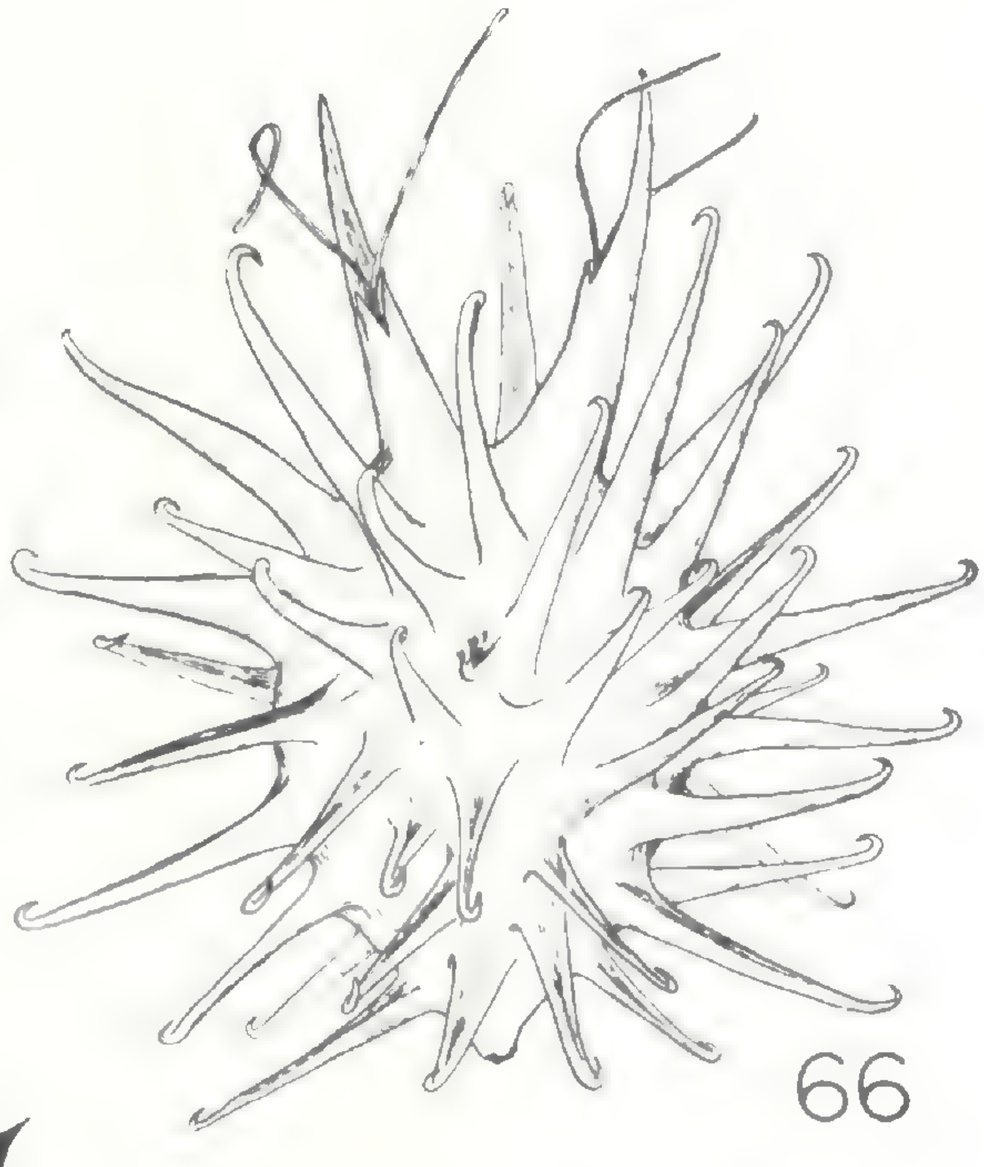

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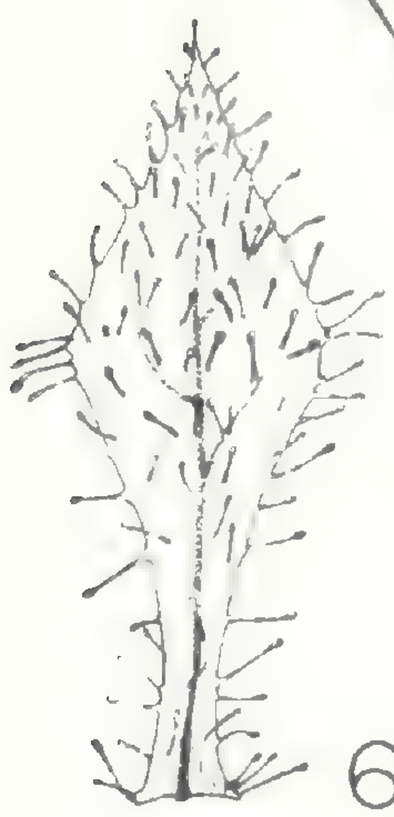

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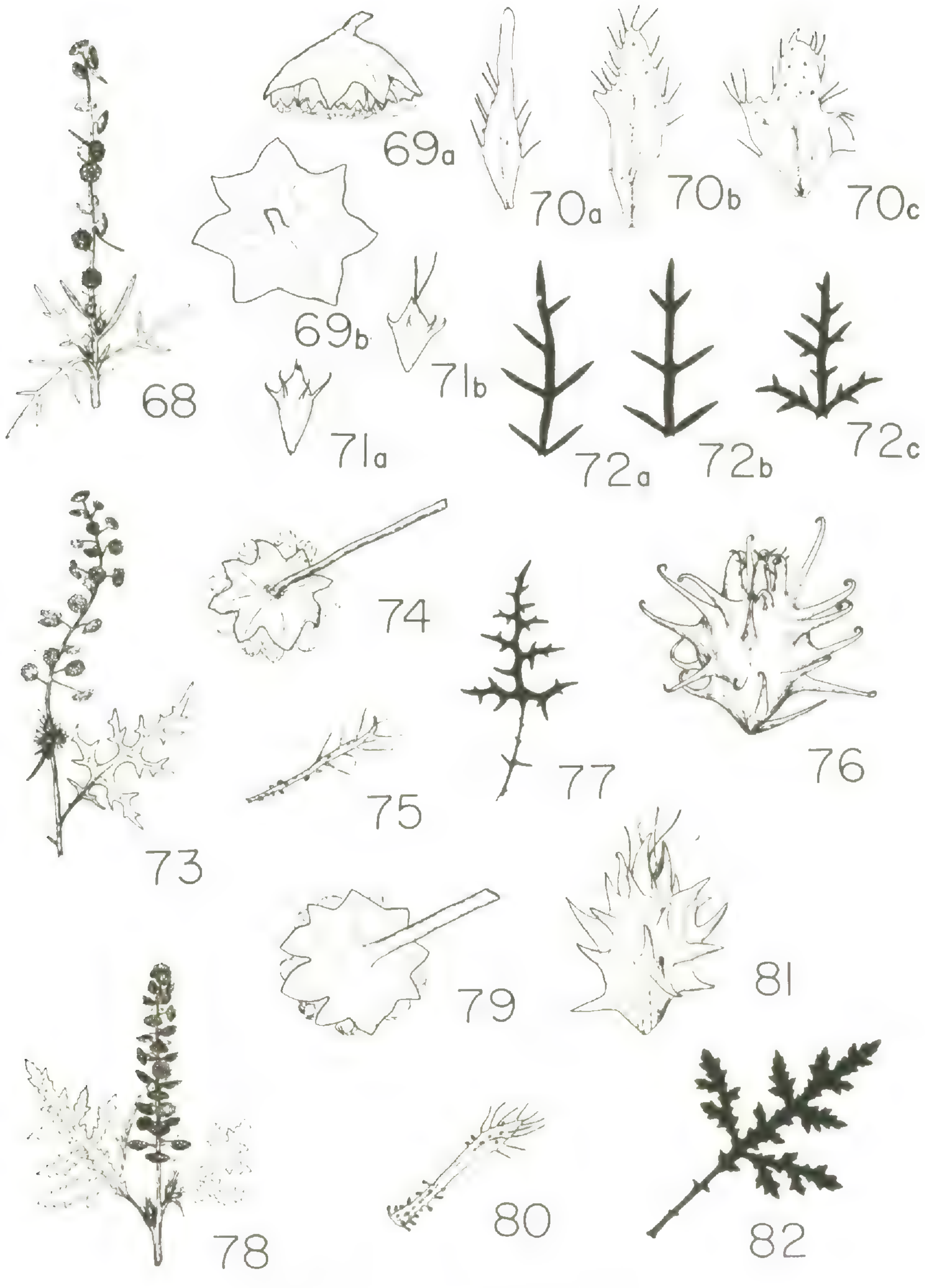
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# THE GENERA OF RHAMNACEAE IN THE SOUTHEASTERN UNITED STATES [1]

GEORGE K. BRIZICKY

RHAMNACEAE A. L. de Jussieu, Gen. Pl. 376. 1789, "Rhamni," nom. cons.
(BUCKTHORN FAMILY.)

Deciduous or evergreen trees, shrubs, or woody vines [exceptionally herbs], unarmed or armed with thorns or stipular spines. Leaves simple, alternate, subopposite, or opposite, petiolate; stipules mostly free, more rarely connate across the axil, usually minute and caducous, sometimes modified to spines [rarely absent]. Inflorescences axillary few-flowered umbel- or corymb-like cymes (sometimes reduced to a solitary flower), or axillary and/or terminal raceme- or spikelike thyrses. Flowers small or minute, regular, perigynous to epigynous, with a distinct floral tube, bi- and/or unisexual by abortion, pediceled or sessile. Floral tube ("hypanthium") patelliform to hemispherical or campanulate [or urceolate to cylindrical], persistent in fruit at least in part; calyx lobes usually 4 or 5, valvate in aestivation, usually deciduous either separately or with the sometimes circumscissile upper part of the floral tube, rarely persistent. Petals 4 or 5, alternate with the calyx lobes, ± concave or hooded or flat, often clawed, enfolding the stamens in aestivation, or wanting. Stamens 4 or 5, opposite the petals, adnate to them at the base and inserted at or below the margin of the disc, smaller and sterile in ♀ flowers; filaments usually subulate, longer or sometimes slightly shorter than the anthers; anthers dorsifixed, usually nonversatile, 2-locular at anthesis, longitudinally dehiscent; pollen usually 3-colporate, suboblate to subprolate, small to medium sized, often ± triangular in polar view, ± smooth to reticulate. Nectariferous disc intrastaminal, hypogynous to epigynous [rarely wanting]. Gynoecium 2- or 3[4]-carpellate, syncarpous, rudimentary in ♂

[1] Prepared for a generic flora of the southeastern United States, a joint project of the Gray Herbarium and the Arnold Arboretum of Harvard University made possible through the support of George R. Cooley and the National Science Foundation and under the direction of Carroll E. Wood, Jr., and Reed C. Rollins. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. **39**: 296–346. 1958) and continued through those in volumes 40–45 (1959–1964). The area covered is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.

The author is indebted to Carroll E. Wood, Jr., for his many valuable suggestions; to J. Rzedowski, Escuela Nacional de Ciencias Biológicas, México, D. F., for supplying references to the distribution of *Berchemia scandens* in Mexico; and to Mrs. Gordon W. Dillon for her help in the preparation of the typescript.

flowers; stigmata 2 or 3 [4] or stigma 1, usually lobed; style 1, often 2- or 3[4]-lobed to -parted; ovary 2- or 3[4]-locular, sometimes incompletely so at the very base [or in the middle, or rarely throughout], the septation diverse; ovules solitary [exceptionally 2] in each locule, basal [or subbasal?], ascendent, anatropous, epitropous or (more commonly) pleurotropous (the raphe lateral) [very rarely apotropous?], 2-integumented, with a thick nucellus, funiculate. Fruit usually a drupe with 2 or 3 [4] dehiscent or indehiscent pyrenes, or with a (1-) 2- or 3-locular dehiscent or indehiscent stone, or rarely a commissurally winged [or unwinged] schizocarp, with [or without] a carpophore.[2] Seed convex and smooth or rarely grooved on the back (abaxial side), with lateral, rarely dorsal, raphe, sometimes minutely [or conspicuously] arillate; endosperm scanty or copious, rarely ruminate, or wanting; embryo "investing," usually large, axial, straight; cotyledons flat or plano-convex; radicle inferior. TYPE GENUS: *Rhamnus* L.

A family of nearly 55 genera and 900 species, of the Tropical and Temperate zones of both hemispheres, the northern limit of the range mostly running between 50° and 55° N. Lat. Five tribes generally are recognized. Intergeneric relationships show many reticulations, and it is likely that further studies will result in a reduction in the number of genera.

The small, generally inconspicuous flowers, which always have a floral tube formed by the fusion of basal parts of the perianth and androecium, are mostly bisexual. Unisexual flowers, with consequent polygamy and/or mono- or dioecism, occur within some genera (e.g., *Berchemia, Gouania, Rhamnus* spp.) but only rarely, if at all, are a character of generic significance. Cross-pollination by hymenopterous, coleopterous, and dipterous insects seems to be the rule, but data are available for relatively few genera and species. Pollen morphology is relatively uniform throughout the family.

[2] Fruits in Rhamnaceae have often been characterized as drupes and or berries and/or capsules. Recently, Vikhireva, on the basis of the gross morphology and histology of the fruits of this family, classified them as syncarpous drupes throughout. Such drupes are in many cases, perhaps in most, closely related to capsules, on the one side, and to schizocarps, on the other, being a link of an evolutionary sequence from syncarpous capsule to syncarpous drupe to schizocarp (*sensu stricto*). It is not surprising, therefore, that among the syncarpous drupes of Rhamnaceae there are forms not only similar to but apparently intermediate to capsules and schizocarps. The classification of forms intermediate to schizocarps seems to be especially difficult, at least in some cases. In this respect, Rusby's suggestion (in Rusby & Jelliffe, *Morphology and Histology of Plants*, pp. 110, 111. 1899) can be helpful. Since schizocarps are commonly provided with appendages for transportation by wind or by mechanical adhesion to passing bodies, "those forms which as above stated are intermediate toward drupes are to be classed in one or the other class, according to whether such appendages for distribution, or that of edible [= fleshy] pericarp [mesocarp], is the more pronounced." In concurrence with both this suggestion and Vikhireva's conclusions, the fruits of Rhamnaceae are classified here as drupes, except those in *Gouania* and its allies, which are regarded as schizocarps.

The structure of the ovary with regard to the number of carpels, the mode of septation ("placentation"), and the fertility or sterility of the septal margins representing the margins of two adjoining connate carpels seems to be a character important for understanding the evolution of the family (see Suessenguth, pp. 31–33). As a rule, only one of the two margins of a carpel forming an ovary locule is fertile, and the sequence of the fertile and sterile margins of carpels or septa in a three-locular ovary can be different in different genera. Consequently, two general situations are possible: in the first case, one of the septa is fertile on both its margins, the second on one, and the third completely sterile (e.g., *Rhamnus* spp.); in the second case, each septum is fertile on one of its margins (e.g., *Ceanothus* spp.).

Basal placentation has generally been regarded as one of the most distinctive features of Rhamnaceae. Prichard confirmed this for at least six genera which he investigated and also remarked, "The ovules do, however, develop from the lateral [slightly incurved] margins of carpels" (p. 103). This agrees with the explanation offered by Suessenguth (*loc. cit.*) and seems to make it rather clear that this basal placentation is one of the variants of axile placentation, or at most a derivative of it. (See, however, Nair & Sarma, p. 54).

Chromosome counts made for eleven genera (55 species) are $2n = 18$, 20, 22, 24, 26, 34, 36, 37, 40, 48, 49, or 50, 72, and 96, suggesting that both aneuploidy and polyploidy have been of importance in the evolutionary development of Rhamnaceae. It is notable that $2n = 24$ is the most frequent chromosome number occurring in at least some species of eight genera, and that both highly polyploid and homoploid genera occur in the family.

In most of our genera the seeds are dispersed mainly by birds and mammals (e.g., *Rhamnus*, *Berchemia*, *Reynosia*, *Sageretia*, *Krugiodendron*), rarely by wind (e.g., *Gouania*) or by water (*Colubrina asiatica*). In some, the fruits themselves are mechanically active ("explosive fruits"), ejecting seeds short distances (e.g., *Ceanothus*, *Colubrina* spp.).

A close relationship of Rhamnaceae to Vitaceae seems to be unquestionable. The relationship to Celastraceae presumed by Prichard and some taxonomists (cf. Suessenguth) is denied by Nair & Sarma (p. 54), who remarked, "It must be noted that floral-anatomically there is very little in common between the two families (see Berkeley, 1953). Further the embryological and palynological data do not support any relationship between the two families. . . ."

Species of several native and exotic genera (e.g., *Paliurus*, *Pomaderris*, *Colletia*) are cultivated as ornamentals. The eastern Asiatic *Hovenia dulcis* Thunb., raisin tree, $2n = 24$, cultivated as an ornamental and for its fleshy, edible rachis and inflorescence branches, has been recorded as escaped and spreading very slowly in Polk County, North Carolina (Freeman). Some species yield wood of local importance (e.g., the tropical African *Maesopsis Eminii* Engl., musizi; the East African *Phyllogeiton Zeyheri* (Sond.) Suesseng., pink or red ivory wood). Fruits, bark, and/or roots of some species are sources of drugs or natural dyes.

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## KEY TO THE GENERA OF RHAMNACEAE

General characters: *woody plants; flowers small, regular, 4- or 5-merous, bisexual, more rarely unisexual; floral tube always developed; petals mostly concave or hooded, often unguiculate, or wanting; stamens 4 or 5, opposite the petals; nectariferous disc intrastaminal; gynoecium syncarpous, the ovary superior to inferior, 2- or 3-locular; ovule solitary in each locule, basal, ascendent; fruit a syncarpous drupe or a schizocarp.*

A. Leaves alternate.
  B. Plants climbing by twining or by tendrils.
    C. Vines climbing by twining; leaves entire, with 9–12 pairs of straightish subparallel veins; ovary superior, 2-locular; fruit a bluish-black ellipsoid to obovoid 1-stoned drupe. . . . . 5. *Berchemia*.
    C. Vines climbing by solitary tendrils near base of peduncle of inflorescence; leaves coarsely and remotely crenate-serrate, with 4–7 pairs of curved, somewhat convergent lateral veins; ovary inferior, 3-

locular; fruit a 3-winged schizocarp ca. 1 cm. broad, splitting along each wing into three 2-winged mericarps. . . . . 9. *Gouania.*

B. Plants erect shrubs or trees.

D. Inflorescences dichotomously branched manifestly peduncled many-flowered axillary and terminal thyrses, the branches becoming club shaped, fleshy, and reddish in fruit; nectariferous disc pubescent; drupe leathery, subglobular, light grayish or brownish, with a thin-coriaceous, indehiscent, 3-locular stone; leaves large, 3-nerved at base, the petiole 2.5–4 cm. long; deciduous ornamental tree sparingly escaped from cultivation. . . . . [*Hovenia* Thunb.]

D. Inflorescences neither dichotomous nor fleshy in fruit; nectariferous disc glabrous; petiole usually short.

E. Drupe fleshy, superior, subtended at base by a flat remnant of the floral tube; inflorescences few-flowered corymb- or umbel-like fascicles, short peduncled to sessile.

F. Branchlets bearing flowers and fruits often fascicled in axils of leaves or leaf scars, usually deciduous; stipules modified to spines; petals hooded, conspicuously clawed; nectariferous disc flat, ± pentagonal, encircling the ovary up to a conspicuous stylopodium; drupe red to brown or black, ellipsoid; stone solitary, hard, sharp pointed, indehiscent; leaves 3-nerved almost to the apex, lateral veins often obscure; cultivated and naturalized deciduous shrub or small tree. . . . . 6. *Ziziphus.*

F. Branchlets not fascicled; stipules caducous; nectariferous disc lining walls of floral tube, free from ovary; stylopodium absent; drupe nearly black, subglobular to almost obovoid, with 3 distinct dehiscent or indehiscent pyrenes; leaves pinnately veined, finely serrulate. . . . . 1. *Rhamnus.*

E. Drupe leathery, semi-inferior, adnate to a cuplike floral tube either at base or to half its length, separating into 3 dehiscent pyrenes or pyrene-like carpels; disc ± annular, encircling the semi-inferior ovary; inflorescences many- to few-flowered thyrses.

G. Inflorescences usually many-flowered corymb- or raceme-like axillary or terminal thyrses longer than the subtending leaves; calyces and elongated filiform pedicels white; petals white, long clawed, much longer than the calyx lobes; leaves usually toothed, 3-nerved at least at base; drupes subglobular or obovoid, distinctly 3-lobed; deciduous low shrubs or subshrubs. . . . . 3. *Ceanothus.*

G. Inflorescences few-flowered contracted axillary thyrses much shorter than the subtending leaves; calyces and pedicels green; petals yellow to greenish or white, very short clawed to sessile, as long as or shorter than the calyx lobes; leaves pinnately nerved and entire or 3-nerved at base and/or serrulate; drupes subglobular, inconspicuously 3-lobed or unlobed; evergreen shrubs or small trees; southernmost Florida. . . 4. *Colubrina.*

A. Leaves opposite and subopposite.

H. Leaves usually acute or short-acuminate at apex, serrulate or serrulate-crenate, ovate; stipules free, caducous; flowers petaliferous, sessile, in slender, spikelike, often panicled axillary and terminal thyrses much longer than the subtending leaves; drupe containing (2) 3 distinct,

flattish, dehiscent pyrenes; small spinescent shrub, occasionally clambering; southeastern Coastal Plain. ..... *2. Sageretia.*

H. Leaves obtuse or rounded, usually notched at apex, otherwise entire; stipules ± connate across the axil, persistent; flowers apetalous, pediceled, in few-flowered axillary cymes much shorter than the subtending leaves or sometimes solitary; drupe subglobular, with a single hard stone; southernmost Florida.

I. Leaves thin-coriaceous, not revolute at margin, ovate to broadly elliptic, obtuse to rounded at base, with 4–6 pairs of conspicuous, slightly curved lateral veins and coarsely reticulated veinlets; stipules connate only at the very base; calyx lobes crested inside. ..... 8. *Krugiodendron.*

I. Leaves stiff-coriaceous, revolute at margins, oblong or oblong-elliptic to narrowly obovate, cuneate to rounded at base, with 6–15 pairs of straightish, usually obscure lateral veins and numerous finely reticulated veinlets (lens!); stipules connate at least half their length; calyx lobes crestless inside. ..... 7. *Reynosia.*

Tribe RHAMNEAE

1. **Rhamnus** Linnaeus, Sp. Pl. 1: 193. 1753; Gen. Pl. ed. 5. 89. 1754.

Deciduous [or evergreen] unarmed [or armed] shrubs or trees [rarely woody vines] with scaly or naked buds. Leaves alternate [to opposite], membranaceous [to coriaceous], pinnately veined, toothed [or entire]. Inflorescences axillary sessile or peduncled umbel-like cymes, sometimes reduced to solitary flowers [or axillary and/or terminal thyrses or rarely racemes]. Flowers small, perigynous, pediceled, bisexual and/or unisexual by abortion, the plants then usually (polygamo-) dioecious. Floral tube ± campanulate [to urceolate]; calyx lobes 4 or 5, greenish or greenish yellow, deciduous separately or with the circumscissile upper part of the floral tube after anthesis. Petals 4 or 5, shorter than calyx lobes, yellowish or whitish, usually broad, nearly ovate or obovate [or sometimes linear to filamentous], emarginate to bilobed at apex [rarely acute], often somewhat different in ♂ and ♀ flowers, usually short clawed, concave to flat [or hooded], inserted at upper margin of disc, or wanting. Stamens 4 or 5, as long as or somewhat longer than petals, sterile and ± rudimentary [or wanting] in ♀ flowers; filaments slightly longer or shorter than anthers; anthers oblong-ovate to ovate in outline, ± cordate at base, sometimes apiculate at apex. Nectariferous disc lining wall of floral tube, thin below, somewhat thickened above. Stigma 3-lobed or stigmata 2–3 and subcapitate-discoid; style simple or 2- or 3[4]-forked; ovary superior, 2- or 3[4]-locular, incompletely so at the very base; ovules epitropous or pleurotropous. Fruit a small subglobular to obovoid, usually black [or dark red, rarely yellow] drupe, with 2 or 3 [4] pyrenes; mesocarp fleshy, with tanniniferous idioblasts or mucilage cavities; pyrenes cartilaginous to somewhat woody, ± convex on abaxial (dorsal), somewhat angular to almost flat on adaxial (ventral) surface, with a distinct adaxial suture, dehiscent or indehiscent. Seed narrowly or broadly obovate to subor-

bicular, plano-convex or lenticular, smooth or longitudinally grooved on abaxial side; seed coat membranaceous, sometimes very thin and closely adherent [or adnate] to endocarp; endosperm fleshy, scanty; embryo large, the cotyledons curved or flat, the radicle short. Germination epi- or hypogeal. (Including *Frangula* Mill.) LECTOTYPE SPECIES: *R. cathartica* L.; typified by S. F. Gray, Nat. Arrang. Brit. Pl. **2**: 621. 1824, who included only this species in sect. *Rhamnus*. (Name from Greek, *rhamnos*, an ancient name of some species of the genus.) — BUCKTHORN.

A genus of 150 (or fewer) species, distributed primarily in the Temperate and Tropical zones of both hemispheres, abundant in eastern Asia and southwestern North America, scarce in Europe and Africa, absent from Madagascar, Australia, Polynesia, and southern South America; three indigenous species in our area.

The four subgenera exhibit reticulate relationships. The most distinctive differences are in the structure of pyrenes and seeds; in this respect subg. PSEUDOFRANGULA[3] is intermediate between subgenera RHAMNUS and FRANGULA (cf. Wolf, pp. 18, 32). Subgenus SCIADOPHILA (Philippi) Benth. & Hook. (including only the Chilean *Rhamnus diffusa* Clos [*Colletia maytenoides* Griseb., *Sciadophila maytenoides* (Griseb.) Philippi]) is poorly known, especially in regard to the structure of pyrenes and seeds, and perhaps represents a distinct, but closely related, genus.

Subgenus RHAMNUS. Winter buds scaly; leaves alternate [to opposite]; flowers usually petaliferous and 4-merous, mostly bi- and/or unisexual; style forked; pyrenes usually dehiscent along the adaxial suture; seeds deeply grooved on the back, with an abaxial raphe on the bottom of the groove; cotyledons thin, curved around the intruded groove; germination epigeal. About 100 species, centered in eastern Asia, a few in Europe and in tropical Africa (exclusive of Madagascar), several in North America. *Rhamnus lanceolata* Pursh, a tall unarmed shrub, with lanceolate leaves and two-carpellate gynoecia, occurs on open wooded slopes, thickets, and glades, usually on calcareous soil, from Alabama and Tennessee west to eastern Texas and Arkansas, north to Nebraska, southern Iowa, southern Wisconsin, Indiana, southern Ohio, south-central Pennsylvania, West Virginia and Virginia. In the western part of the range var. *lanceolata*, with the leaves short-pubescent on the lower surface, seems to predominate, while in the eastern and southeastern part var. *glabrata* Gleason, with the leaves glabrous or promptly glabrate, appears to prevail. The status of these variants needs further study. The European *R. cathartica* L., common buckthorn, $2n = 24$, a spinescent shrub or small tree with 3- or 4-carpellate gynoecia, has become naturalized in Canada and from the Northeastern States south to Virginia.

Subgenus PSEUDOFRANGULA (Grubov) Brizicky. Winter buds scaly; leaves alternate; flowers apetalous, (4)5-merous, bi- and/or unisexual;

[3] **Rhamnus** L. subg. **Pseudofrangula** (Grubov) Brizicky, stat. nov. *Rhamnus* L. sect. *Pseudofrangula* Grubov, Not. Syst. Leningrad **12**: 125. 1950. TYPE SPECIES: *R. alnifolia* L'Hér.

style forked; pyrenes indehiscent; seeds not grooved, the raphe abaxial; cotyledons thin, ± plane; germination epigeal. Four species, one North American and three eastern Asiatic. *Rhamnus alnifolia* L'Hér., a low shrub with 3-carpellate gynoecia, occurs in swamps, low woods, and meadows, often on calcareous soil, from Newfoundland to north-central Alberta, British Columbia, and Washington, south to central California and northeastern Oregon, Idaho, Wyoming, Nebraska, Iowa to New Jersey, and West Virginia. It was formerly known from Cedar Creek, Campbell County, Tennessee, but this locality is now covered by Norris Lake. *Rhamnus Ishidae* Miyabe & Kudo, apparently closely related to our species, is endemic on Hokkaido, Japan; *R. Arnottiana* Gardner is endemic in Ceylon; and *R. purpurea* Edgew. is known from the Himalaya and adjacent China. The few species and their present distribution suggest the antiquity of this group.

Subgenus FRANGULA (Mill.) Reichenb. Winter buds naked; leaves alternate; flowers petaliferous, 5-merous, bisexual; style simple; pyrenes indehiscent; seeds not grooved, the raphe lateral; cotyledons plane, thickish; germination hypogeal. About 40 species, primarily American (26 species), centered in California and Mexico, occurring southward to Peru and Brazil, with one species in the West Indies; the remaining species mostly in eastern Asia, a few in Europe, North Africa, and the Azores. *Rhamnus caroliniana* Walt., Indian cherry, $2n = 24$, a shrub or small tree, the gynoecia 3-carpellate, occurs in low woodland in valleys along streams, on rocky open wooded slopes, upland ridges, thickets, and glades, commonly on limestone outcroppings, from Florida (Charlotte County on the west and Orange County on the east coast) to westernmost Texas, north to western Virginia, West Virginia, Ohio, Indiana, Illinois, and Nebraska. Two variants which occur throughout this range (although one may be prevalent locally) have sometimes been recognized as var. *caroliniana*, with the leaves glabrous or glabrescent beneath, and var. *mollis* Fern., with the leaves permanently pubescent ("velvety") on the lower surface. *Rhamnus caroliniana* is closely related to *R. betulifolia* Greene, of the southwestern United States and Mexico; both "are interpreted as derivatives of a stock which migrated from farther south and which also probably gave rise to such a species as *R. Purshiana* DC., now distributed from northern California to Washington" (McVaugh). The European *R. Frangula* L., alder-buckthorn, $2n = 20, 22, 26$, a shrub or small tree, the gynoecia 2-carpellate, has become naturalized at least in the Northeastern States, south to New Jersey.

Subgenus FRANGULA differs from our other subgenera in the mucilaginous walls of the epidermal cells and the presence of mucilage ducts in the collenchyma of veins of the leaves and in the fruits; in the uniseriate, several-celled hairs (as against unicellular); and in the somewhat different wood anatomy (cf. Record). On these bases the subgenus is often segregated (especially in Europe) as a distinct genus, *Frangula* Mill. Since, however, *Rhamnus* as a whole seems to have been inadequately studied,

especially with regard to its tropical members, generic segregation appears to be somewhat premature.

The genus is poorly known in regard to its biology, floral morphology, and anatomy. The bisexual flowers of *R. Frangula* have been recorded as proterandrous. Chromosome counts have been made for seven species. Four species of subg. RHAMNUS have $2n = 24$, and one (the tropical African *R. prinoides* L'Hér.), $2n = 34$; two species of subg. FRANGULA have $2n = 24$ and $2n = 20, 22, 26$. Two different forms of karyotype not corresponding to the subgeneric divisions have been found (cf. Dolcher). Fruit dispersal is mostly by birds.

The genus is closely allied to *Sageretia* Brongn.

A number of species are grown as ornamentals and/or hedge plants (e.g., *Rhamnus cathartica*, *R. Frangula*, *R. Purshiana*), and some yield wood of local importance (e.g., *R. Frangula*, *R. cathartica*) or drugs (*R. Purshiana*, *R. Frangula*, *R. cathartica*). *Rhamnus caroliniana* and *R. lanceolata*, as well as several species of the Pacific States (e.g., *R. californica* Eschsch., *R. Purshiana*) are important honey plants. Fruits of *R. alnifolia* are said to be poisonous. At least *R. alnifolia*, *R. cathartica*, *R. Frangula*, and *R. lanceolata* are known to be the alternate host for *Puccinia coronata* Corda, crown rust of oats.

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Under family references see GEMOLL (pp. 371–375), HERZOG (pp. 174–199), JUEL, MIERS (pp. 232–250), PRICHARD (pp. 90–93), RECORD (p. 18), SARGENT (pp. 722–726), SUESSENGUTH (pp. 59–71), VIKHIREVA (1951; 1952, pp. 250–255), WEBERBAUER (pp. 409, 410), and WEST & ARNOLD (p. 139).

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2. **Sageretia** Brongniart, Mém. Fam. Rhamn. 52. 1826.

Evergreen [or deciduous] spinescent [or unarmed] shrubs [or small trees]. Leaves opposite or subopposite, small [to rather large], thin-coriaceous [rarely coriaceous], pinnately veined, with 3–5 (6) pairs of

primary veins, serrulate [or entire]. Inflorescences terminal and axillary interrupted spikelike [very rarely raceme-like] often panicled thyrses [or the flowers glomerulate to solitary in leaf axils]. Flowers minute, 5-merous, bisexual, sessile [or very rarely pediceled], 2-bracteolate at base. Floral tube short-campanulate to patelliform [or hemispherical to urceolate (?)]; calyx lobes somewhat fleshy, keeled medially on inner surface, deciduous. Petals whitish, obovate, concave [or cucullate], minutely apiculate and often notched at apex, obscurely [or distinctly] unguiculate, much shorter than calyx lobes. Stamens slightly longer than petals; anthers ovate in outline, dorsifixed near base. Nectariferous disc fleshy, collar-like, with irregularly crenate margin, confluent with floral tube at base [or distinct to base], encircling the ovary. Stigmata 3, small, subcapitate, sometimes ± confluent adaxially; style short, stout, 3-sulcate; ovary superior, 3-locular; ovules pleurotropous. Fruit a small, subglobular [to obovoid], purplish-black drupe with (2) 3 pyrenes; mesocarp fleshy [or leathery], thin; pyrenes thin-cartilaginous, dorsiventrally much compressed, obliquely obcordate, dehiscent along adaxial suture and upper half of the abaxial median.[4] Seed rather flat, obliquely obcordate, slightly keeled submedially on ventral surface, orange-brown [or light brown], usually shining; seed coat thin, crustaceous; endosperm scanty; cotyledons suborbicular-obcordate, thin, the radicle minute. LECTOTYPE SPECIES: *S. theezans* (L.) Brongn.; see A. Rehder, Bibliogr. Cult. Trees Shrubs 436. 1949. (Named after Augustin Sageret, 1763–1851, French horticulturist and plant physiologist.)

A primarily tropical genus of nearly 30 species, centered in eastern Asia, extending south to Indonesia and northeastern Australia, west to southern Arabia and northeastern Africa; three species in North America, one occurring from Mexico south to Peru, Paraguay, and northern Argentina. *Sageretia minutiflora* (Michx.) Mohr,[5] a trailing or straggling shrub usually six to ten feet tall, with polymorphic, relatively small leaves and very fragrant flowers, occurs on calcareous sandy soils, rocky bluffs, open dry copses, and margins of low rich woods (here sometimes ascending high

[4] The pyrenes of *Sageretia* have generally been described as indehiscent, but as early as 1907 Sprague stated that in at least *S. Brandrethiana* Aitch. the pyrenes are dehiscent. Recently, Grubov (Fl. USSR **14**: 638. 1949) mentioned dehiscent pyrenes as a generic character in *Sageretia*, and Vikhireva (p. 258) described the dehiscence of pyrenes in *S. laetivirens* (Kom.) Gontsch. I have found the pyrenes dehiscent (when dried) in *S. minutiflora* and *S. elegans*, of the New World, and in *S. Henryi* Drumm. & Sprague, *S. lucida* Merr., and *S. spiciflora* (A. Rich.) Chiov. ex Hutch. & Bruce, of the Old World.

[5] *Sageretia minutiflora* (Michx.) Mohr, Contr. U. S. Natl. Herb. **6**: 609. 1901. The authorship of this combination has usually been attributed to Trelease (1889, p. 367). However, Trelease's note under *S. Michauxii* Brongn., "If the specific name given by Michaux is to be retained, the plant becomes *S. minutiflora* (Michx.)," should be regarded as an incidental mentioning because Trelease himself did not adopt this name in either of his revisions of Rhamnaceae. Therefore, according to the International Code of Botanical Nomenclature (ed. 1961, Art. 34, Note 2) Trelease's mention of the combination does not constitute its valid publication.

trees) on the Coastal Plain from southern Florida (Lee County on the west and Brevard County on the east coast) to Mississippi and South Carolina. This species seems to be more closely related to the Mexican-South American *S. elegans* (HBK.) Brongn. and the wide-ranging Old World *S. theezans*, $2n = 24$, than to the Texan-Mexican *S. Wrightii* S. Wats.

The genus seems to be closely related to *Rhamnus*, combining in its fruits the dehiscent pyrenes of subg. RHAMNUS, the rather flat pyrenes and seeds of subg. PSEUDOFRANGULA, and the lateral raphe of subg. FRANGULA. It differs from *Rhamnus* especially in the nectariferous disc which is almost completely free from the floral tube.

The fruits of some species, e.g., *Sageretia theezans*, are said to be edible. Leaves of the same species are reportedly used as a substitute for tea in China.

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3. **Ceanothus** Linnaeus, Sp. Pl. 1: 195. 1753; Gen. Pl. ed. 5. 90. 1754.

Deciduous [to evergreen] unarmed [or spinescent] shrubs [rarely small trees], with 3-lacunar nodes. Leaves alternate [or opposite], membranaceous [or coriaceous], serrulate or crenate-serrulate to subentire [or serrate, or spinulose], 3-nerved at base [or pinnately veined]; stipules small, thin, deciduous [or ± corky, persistent]. Inflorescences terminal and/or axillary, peduncled, raceme- or corymb-like thyrses composed of few-flowered umbel-like cymes, or the flowers solitary or in few-flowered cymes in the leaf axils at the top of leafy branchlets. Flowers small, usually 5-merous [exceptionally 6–8-merous], perigynous, bisexual, white [blue to lavender], slender pediceled, the calyx and pedicels colored like the petals. Floral tube shallow, cupular-turbinate to hemispherical; calyx lobes triangular, petaloid, usually ± inflexed, deciduous. Petals hooded, clawed, longer than calyx lobes, ± spreading, inserted at base of disc. Stamens exserted, equalling or exceeding petals; anthers ovate-cordate in outline. Nectariferous disc annular, tumid, often distinctive in color, encircling the upper portion of the ovary. Stigmata 3, small, subcapitate; style 3-forked in the upper third to half; ovary semi-inferior, 3-locular, incompletely so at the very base; ovule pleurotropous. Fruit a small purplish-black drupe, ± 3-lobed or -cornered, smooth or crested [ridged or horned] on back of lobes or corners at their tops, supported by and adnate to the persistent base of floral tube, containing 3 coherent pyrenes; mesocarp thin, fleshy or ± leathery; pyrenes cartilaginous, obovate in

outline, convex on abaxial, angular on adaxial surface, explosively dehiscent along adaxial suture and upper portion of the abaxial median, ejecting seeds. Seed narrowly to broadly obovoid, plano-convex, dark brown to black, smooth, shining, with a lateral raphe, minutely arillate at base; seed coat crustaceous; endosperm fleshy, scarce; embryo large, the cotyledons broadly elliptic- to suborbicular-cordate, flat, thin, the radicle minute. TYPE SPECIES: *C. americanus* L.; typified by the removal of two of the three original species to other genera; see A. Brongniart, Mém. Fam. Rhamn. 62, 64. 1826. (Name from Greek, *keanothos*, the name of some prickly plant mentioned by Theophrastus, applied to this genus by Linnaeus.) — REDROOT.

An exclusively American genus of nearly 55 species, distributed from Guatemala (one species) north to southern Canada, centered in California (44 species). Two natural, very distinct sections, CEANOTHUS, with ca. 36 species, and CERASTES S. Wats., with 19 species, are recognized. Four species of sect. CEANOTHUS occur in our area.

*Ceanothus americanus* L., New Jersey tea, $2n = 24$, a low shrub or subshrub up to a meter tall, with mostly ovate leaves and axillary, mostly raceme-like thyrses on elongated leafless peduncles, occurs in woods, hillsides, ravines, and prairies from southern Quebec and southern Ontario west to Minnesota and Nebraska, south to Texas and northern Florida. Its slender-branched variant with leaves usually 2–4 cm. long (in Gleason's delimitation), known as var. *intermedius* (Pursh) Torr. & Gray,[6] seems to represent the species on the sterile or sandy ground of the Coastal Plain, from Massachusetts south to central Florida and west to Louisiana and Arkansas. Another variant, var. *Pitcheri* Torr. & Gray, with lower leaf surface densely permanently velutinous, occurs scattered throughout the range of the species, but appears to be predominant in the prairies from Illinois west and southwest. Dried leaves of this species were used as a substitute for tea during the American Revolution. *Ceanothus serpyllifolius* Nutt., a low, diffusely branched shrub 20–45 cm. tall, with ovate-elliptic leaves 0.6–1.25 cm. long and axillary, few-flowered, corymb-like thyrses on elongated leafless peduncles, occurs in a few scattered localities in pinelands on the Coastal Plain of Georgia and Florida, south to Volusia County. It is "closely allied to *C. americanus* var. *intermedius*, from which it differs chiefly in size" (Trelease, 1897, p. 410). The specific status of this plant is questionable.

*Ceanothus herbaceus* Raf. (*C. ovatus* Desf.), a shrub up to 1 m. tall, with oblong-elliptic to elliptic-lanceolate leaves and terminal, short-

[6] This variant has been variously delimited with regard to the leaf size: e.g., leaves mostly under 1 inch long (Trelease, 1888, 1897; McMinn in Van Rensselaer & McMinn); 2–4 cm. long (Gleason, New Britt. Brown Illus. Fl. NE. U. S. 2: 514. 1952); or 2–6 cm. long (Fernald, Gray's Man. Bot. ed. 8. 993. 1950). Such different delimitations produce rather different ranges for this variety. Until extensive population studies are made and the results carefully evaluated, the limits of this variant, the existence of a distinct range, and, consequently, its varietal status will remain uncertain.

peduncled, corymb-like thyrses, occurs in upland and rocky prairies, rocky woodland, open rocky places, calcareous bluffs, and dry ground, from southern Quebec to southern Manitoba, North Dakota, and Colorado, south to Nebraska, Kansas, Oklahoma, and Texas (locally in Eddy County, in southernmost New Mexico), Arkansas, locally in central Tennessee (White County), Kentucky, West Virginia, northernmost Virginia (Arlington County), the District of Columbia, and New Jersey, and, according to McMinn, in Lake County, Florida (the specimen *Nash 1041* not seen by the writer). A variant with the lower surface of the leaves permanently densely villous, has been regarded as *C. herbaceus* Raf. var. *pubescens* (S. Wats.) Shinners (*C. ovatus* var. *pubescens* S. Wats.), but Soper showed that this variant, "which has generally been considered as having a more western distribution, occurs within the range of the species even as far east as the Great Lakes and northeastern Massachusetts, and therefore should be considered "as merely a pubescent form."

*Ceanothus microphyllus* Michx., a low, diffuse shrub or subshrub 15–60 cm. tall, with leaves 3–7 mm. long, alternate and often also fasciculate in the leaf axils, and small terminal corymb- or raceme-like panicles, occurs in dry pine- or oak-woods on the Coastal Plain from Highlands County, Florida, to southwestern Alabama and southern Georgia. The terminal inflorescences suggest a close relationship to *C. herbaceus*.

The flowers of *Ceanothus* usually are 5-merous and the floral anatomy very uniform, although 6–8-merous flowers with an additional vascular bundle to each extra floral segment occur regularly in *C. Jepsonii*.

The genus is homoploid, the chromosome number being invariably $2n = 24$ in the 34 species investigated (Nobs); the karyotype is also uniform. Intersectional hybrids are extremely rare and always sterile, indicating a strong genetic barrier between the sections. On the contrary, intrasectional interspecific hybrids, both natural and artificial, are very numerous.

The roots of some species (e.g., *Ceanothus americanus*, *C. velutinus* Dougl.) are known to develop mycorrhizal nodules in great abundance. The presence of nitrogen-fixing bacteria in these nodules seems to be questionable (cf. Furman).

The fossil records indicate that *Ceanothus* has been present on the Pacific slope of North America at least since the Oligocene and that the differentiation of the two sections of the genus might already have occurred in the Miocene (cf. Nobs, p. 78).

The genus seems to be closely related to *Colubrina* Brongn.

Numerous species and hybrids of *Ceanothus* are valuable ornamentals. *Ceanothus americanus*, *C. ovatus*, and *C. coeruleus* Lag. (*C. azureus* Desf.), the earliest species introduced into cultivation, provided the basis for many attractive garden hybrids. Many species are important as sources of food and shelter for wildlife; some can also be used for erosion control.

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Under family references see GEMOLL (pp. 375–380), JUEL, PRICHARD (pp. 93–

95), SARGENT (pp. 726–729), SUESSENGUTH (pp. 72–82), TRELEASE (1897, pp. 409–417), and VIKHIREVA (1951; 1952, pp. 262–265).

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4. **Colubrina** L. C. Richard ex Brongniart, Mém. Fam. Rhamn. 61. 1826. nom. cons.

Unarmed or spinescent evergreen shrubs or small [very rarely large] trees. Leaves alternate [rarely opposite], membranaceous to subcoriaceous [or coriaceous], pinnately nerved or 3-nerved from base, entire or finely [to coarsely] toothed, often with small, round glands scattered on lower surface and/or 1 or 2 glands at base of blade; stipules minute, free, caducous [or connate in the axil, persistent]. Inflorescences axillary cymes or small thyrses, sessile and umbel-like or short peduncled, few flowered, and corymb-like [or flowers rarely axillary, solitary]. Flowers small, usually 5-merous, bisexual, perigynous. Floral tube hemispherical; calyx lobes triangular-ovate, spreading, conspicuously keeled on inner surface, deciduous. Petals greenish yellow to yellow or white, cucullate, sessile to short-unguiculate, shorter than calyx lobes, inserted at exterior margin of disc. Stamens nearly as long as petals; anthers ovate in outline, subbasifixed, introrse. Nectariferous disc large, fleshy, pentagonal or indistinctly shallowly 10-lobed, filling the floral tube, surrounding the ovary and adnate to its lower half. Stigmata 3, small, obtuse; style slender, 3-lobed to -fid; ovary semi-inferior, 3-locular; ovules pleurotropous. Fruit a subglobular, ± 3-lobed orange-red to black drupe supported at the base by the adnate floral tube; mesocarp thin and dry [or ± fleshy]; stone cartilaginous or crustaceous, 3-locular, splitting septicidally into 3 pyrene-like carpels dehiscent along the whole adaxial suture and halfway down abaxially. Seeds broadly obovate in outline, convex on abaxial, flattish-angular on adaxial side, brown to black, usually lustrous, smooth or sometimes pitted, sometimes with a minute aril at base; seed coat coriaceous to almost bony; endosperm fleshy, thick; embryo straight, axial, the cotyledons flat, ± fleshy, elliptic-suborbicular, the radicle small. (Including *Cormonema* Reissek ex Endl., and *Hybosperma* Urb.) LECTOTYPE SPECIES: *C. ferruginosa* Brongn. = *C. arborescens* (Mill.) Sarg.; see N. L. Britton. N. Am. Trees 681. 1908. (Name apparently derived from *bois couleuvre*, snakewood or serpent tree, the French name of the type species on Martinique, translated into Latin as *Arbor colubrina* by Jacquin. Select. Stirp. Am. Hist. 75. 1763.)

An almost pantropical genus of nearly 30 species, centered in tropical America, with a few species in southeastern Asia, Malesia, tropical Australia and Polynesia (to Hawaii), with one species in coastal East Africa and the Mascarene Islands; three indigenous and one naturalized species in our area. The genus has recently been subdivided into subg. COLUBRINA, with entire, pinnately veined leaves, and subg. SERRATARIA M. C. Johnst., with glandular-serrate leaves often 3-nerved at base. Each subgenus comprises two sections.

Subgenus COLUBRINA sect. COLUBRINA, with branchlets not spinescent, glands scattered on the lower leaf surface, and pyrene-like parts of the stone dehiscing explosively, includes about five tropical American species. *Colubrina arborescens* (*C. ferruginosa*, *C. Colubrina* (Jacq.) Millsp.), wild-coffee, a shrub or small tree with rusty tomentose branchlets, ovate to elliptic leaves 5–15 cm. long, and stout-pediceled drupes, known from the West Indies and Mexico to Guatemala, occurs in the hammocks of southernmost peninsular Florida and on the Florida Keys. Section VELLOZIA M. C. Johnst., with branchlets spinescent, leaf blades biglandular near the base, and dehiscence of the fruits not explosive, includes seven species, all tropical American. *Colubrina elliptica* (Sw.) Brizicky & Stern (*C. reclinata* (L'Hér.) Brongn.), soldierwood or nakedwood, a shrub or small tree with puberulent branchlets, ovate-elliptic to elliptic or obovate leaves, and slender-pediceled drupes, of the West Indies and Mexico to Venezuela, occurs in southernmost peninsular Florida (Dade County) and on the Florida Keys. This species "seems to be intermediate between the two sections and to link them together" (Johnston, p. 91).

Subgenus SERRATARIA M. C. Johnst. sect. SERRATARIA, with leaves more or less evenly pinnately veined [or 3-nerved at base] and fruits thick walled and tardily dehiscent, is a primarily West Indian-Mexican group of nine species, extending north to California, southern Arizona, Texas, and southernmost Florida. The West Indian *Colubrina cubensis* (Jacq.) Brongn. is represented in hammocks of southern peninsular Florida by var. *floridana* M. C. Johnst., a shrub or tree with leaves narrowly elliptic-oblong to lance-oblong, 5–10 cm. long and 1.2–3.8 cm. broad, finely tomentose on both surfaces, rounded or obtuse at apex, rounded or broad-cuneate at base, with obscurely crenulate-serrulate, somewhat revolute margins. Section BARCENA (Duges) M. C. Johnst., including two Mexican and five Old World species, is represented in the coastal hammocks of southernmost peninsular Florida (north to Palm Beach County) and on the Florida Keys by the naturalized *C. asiatica* (L.) Brongn., a glabrous shrub with weak diffuse or prostrate branches (rarely erect and treelike) with ovate, finely crenate-serrulate leaves 3-nerved at base. The species is widely distributed in the tropics of the Old World, in Asia, Malesia, the Pacific islands, tropical Australia, the Mascarene Islands, and coastal East Africa, and is naturalized in tropical continental America and the West Indies. Seeds of this species float and are distributed by sea currents.

The genus is closely related to *Ceanothus*.

The close-grained, hard and heavy wood of some species (e.g., *C. arborescens*, *C. elliptica*) is of some local importance.

REFERENCES:

Under family references see GEMOLL (pp. 380–382), SARGENT (pp. 729–731), SUESSENGUTH (pp. 85–89), TRELEASE (1897, p. 418), VIKHIREVA (1952, pp. 265, 266), and WEST & ARNOLD (pp. 136, 137).

BRIZICKY, G. K., & W. L. STERN. Notes from the S. J. Record Memorial Collection. II. Trop. Woods **109**: 95, 96. 1958. [*C. elliptica* the correct name instead of *C. reclinata*.]

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Tribe PALIUREAE Reisseck [7]

5. **Berchemia** Necker ex De Candolle, Prodr. **2**: 22. 1825, nom. cons. prop.

Glabrous, deciduous, twining woody vines [or shrubs to small trees]. Leaves alternate, membranaceous, pinnately veined, with 9–12 pairs of slightly curved, subparallel primary veins, entire, often wavy. Inflorescences raceme-like thyrses composed of few-flowered, peduncled to subsessile corymb-like terminal cymes (sometimes also occurring in the axils of a few leaves just below the thyrse). Flowers small, 5-merous, perigynous, unisexual by abortion [or bisexual?], the plants apparently dioecious. Floral tube saucer- to shallowly cup-shaped; calyx lobes considerably longer than floral tube. Petals greenish white, obovate or oblanceolate, somewhat concave, ± acute at apex, not clawed in ♂, often very shortly clawed in ♀ flowers, nearly as long as [or somewhat shorter than] calyx lobes, inserted at the exterior margin of the disc. Stamens longer than petals in ♂, shorter and sterile in ♀ flowers; anthers ovate in outline, slightly cordate, dorsifixed near base. Nectariferous disc fleshy, filling floral tube, pentagonal, broad and flat in ♂, narrow with somewhat raised interior margin and encircling ovary base in ♀ flowers. Gynoecium rudimentary in ♂ flowers; stigmata 2, small, subcapitate-discoid; style narrowly conical, usually short-bifurcate; ovary superior, 2-locular, the 2 septa distinct, overlapping each other and extending to opposite ovary wall, accumbent; ovules probably at first epitropous, later changing to pleurotropous during development. Fruit a small, bluish-black, ellipsoid to narrowly obovoid, apiculate single-stoned drupe, supported at base by remnant of floral tube; mesocarp fleshy, often juiceless, thin; stone 2-

[7] The tribe Paliureae Reisseck in Endlicher (Gen. Pl. 1095. 1840) was originally composed of two genera, *Paliurus* Mill. and *Ventilago* Gaertn. In 1862, Bentham and Hooker (Gen. Pl. **1**: 372) established the tribe Ventilagineae to include *Ventilago* and *Smythea* Seem. and placed *Paliurus* in the new tribe Zizipheae. Inclusion of *Paliurus*, the type genus of the tribe Paliureae, in Zizipheae by Bentham and Hooker makes the latter name illegitimate. The correct name for this tribe is Paliureae, and the tribe is to be taxonomically emended to include all the genera of Zizipheae.

locular, bony, thickish, 1- or 2-seeded, indehiscent. Seed subcylindric-ovoid; seed coat membranaceous, thin, adherent and partly adnate to endocarp; endosperm fleshy, scarce; cotyledons oblong, plane, parallel with partition, the radicle short, slightly curved. (*Oenoplea* (Pers.) Michx. ex Hedw. f., nom. rejic. prop.; see Taxon 12: 170. 1963.) TYPE SPECIES: *B. volubilis* (L. f.) DC. = *B. scandens* (Hill) K. Koch. (Name said to commemorate either Nikolaus Berghem, alias Berchem, 1624–1683, a Dutch landscape, plant, and animal painter, or Berthout van Berchem, a contemporary of Necker.)[8]

A primarily tropical genus of 22 (or fewer) species, all except one of Asia (Japan to Afghanistan, south to Java, Celebes, and Timor). The single American species, *Berchemia scandens*, supple-jack or rattan vine, occurs in hammocks, in rich or low woods, or in swamps from southernmost peninsular Florida west to Texas, north and northeast to Arkansas, southern Missouri, Tennessee, and Virginia; disjunct in southern Mexico (Chiapas) and Guatemala (Baja Verapaz). It is "one of the many vines which semi-strangle trees; the tree trunks sometimes nearly grow over this vine, thus producing an ill-shaped non-merchantable trunk" (Brown).

The genus seems to be more or less closely related to *Rhamnella* Miq., *Berchemiella* Nakai, and *Chayadaia* Pitard, all small genera of the Old World. The primarily East African *Phyllogeiton* (Weberb.) Herzog, comprising two species, has sometimes been included in *Berchemia*, but such a close relationship has not been convincingly demonstrated.

A few Asiatic species are sometimes grown as ornamentals. A basic, karyophilic stain, berchemine, was recently obtained from the crushed berries of *Berchemia lineata* (L.) DC.

REFERENCES:

Under family references see BROWN (pp. 178, 179), HERZOG (pp. 166–168), SUESSENGUTH (pp. 141–145), TRELEASE (1897, pp. 404, 405), and VIKHIREVA (1952, p. 259).

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LEISNER, R. S. An unusually large specimen of *Berchemia scandens*. Jour. Elisha Mitchell Sci. Soc. 73: 448. 1957. [Stem 2.4 in. in diameter, age approximately 32 years.]

METCALF, F. P. Relationships between Chinese and Indian *Berchemia*. Peking Nat. Hist. Bull. 16: 17–28. *map*. 1941. [Number of eastern Asiatic spp. reduced to 9.]

[8] There were, however, two of Necker's contemporaries with the same name: Berthout van Berchem, *père*, and Berthout van Berchem, *fils*, both active members of the Society of Natural History in Lausanne, Switzerland. The father was the author of a few articles on agriculture (e.g., on cultivation of potatoes and on soils); the son seems to have been a more prominent zoologist (mammalogist) and chemist.

6. **Ziziphus** Miller, Gard. Dict. Abr. ed. 4. 1754.

Deciduous [or evergreen] shrubs or small trees [rarely woody vines], armed with often unequal stipular spines [or ± axillary solitary or paired thorns, or rarely unarmed]; a few deciduous branchlets resembling pinnate leaves often fascicled in the leaf axils. Leaves alternate [rarely subopposite to opposite, or fascicled], 3-nerved to or almost to the apex [or only at base, or pinnately nerved throughout], crenate-serrulate [to crenate-serrate or entire]; stipules modified to spines [or minute, caducous]. Inflorescences axillary, few-flowered, subsessile to sessile [pedunculed], corymb-like cymes [or terminal or axillary thyrses]. Flowers small, usually 5-merous, perigynous but appearing subepigynous, bisexual, usually yellow. Floral tube shallow, subpatelliform [to hemispherical]; calyx lobes keeled medially and swollen at apex within, deciduous. Petals hooded, unguiculate, shorter than the calyx lobes [rarely wanting]. Stamens somewhat longer than petals; anthers introrse [rarely extrorse], ovate to elliptic in outline. Nectariferous disc fleshy, ± flat, ± pentagonal [or ± 10-lobed], surrounding ovary and ± adherent to it. Stigmata *2* [3], small, subcapitate-discoid; style *2*[3]-furcate, swollen toward base into a stylopodium separated from ovary by a shallow groovelike constriction; ovary appearing to be inferior or semi-inferior (becoming superior in fruit), immersed to the stylopodium in the disc, *2*[3]-locular [or incompletely so], the septa meeting in the center, connate [or distinct]; ovules pleurotropous, basal (Prichard) or subbasal (Nair & Sarma). Fruit an ellipsoid, ovoid to slightly obovoid [or subglobular], dark-red to black single-stoned drupe, 1.5–3[–5] cm. long; mesocarp fleshy; stone bony, ovoid to narrowly ellipsoid, sharply pointed at apex or at both ends, smooth or furrowed, *2*[3]- or 1-locular by abortion, 1-seeded, indehiscent. Seed elliptic in outline, nearly plano-convex, the raphe lateral; seed coat thin, membranaceous; endosperm fleshy, scanty; embryo straight, the cotyledons large, thick, plane, the radicle small. LECTOTYPE SPECIES: *Rhamnus Ziziphus* L. = *Z. Jujuba* Mill.; see Britton & Wilson, Sci. Surv. Porto Rico Virgin Is. **5**(1): 535. 1923. (Latin name of the type species, first introduced by Pliny; etymology obscure.) [9]

A pantropical genus of nearly 100 species, extending locally into the Temperate Zone; centered in southeastern Asia and in tropical America, where the genus ranges from southern Brazil, Paraguay, northern Argentina, and Peru north to the West Indies, Mexico, and the southwestern United States. Although the species of the New World form a group rather distinct from those of the Old (Johnston), no subgeneric categories have

[9] The name has been designated by various authors as being derived from Old Phoenician, *zizuf*; Arabic, *zezaf* or *zefzaf*; Persian, *zizafun*; and Greek, *ziziphos*. According to Löw (Fl. Juden 3: 139. 1924) the plant, which was first introduced into Rome from Syria by the end of the reign of the Emperor Augustus, in the first century A.D., brought its name *ziziphus* from there. This name was further introduced into some European and Oriental languages from Hebrew, from which the Greek word *zizyphos* was also derived.

been established yet. The Old World group is represented in our area by the cultivated and naturalized *Ziziphus Jujuba* Mill. (*Z. Ziziphus* (L.) Karst.), Chinese or common jujube, $2n = 24, 26, 40, 48, 74, 96$, occurring rarely in thickets and on roadsides on the Coastal Plain from Alabama to Louisiana. *Ziziphus mauritiana* Lam. (*Z. Jujuba* Lam., not Mill.), Indian jujube, $2n = 48$, differing in the leaves densely tomentose beneath, is also cultivated in the southern part of our area for its edible fruits.

Bees are regarded as common pollinators, and cross-pollination seems to be the rule. Although self-pollination and -fertilization sometimes occur, the fruits in such cases are small and tend to drop off prematurely. Parthenocarpy and (rarely) polyembryony have been recorded in *Z. Jujuba*.

The genus seems to be closely related to the Asiatic-South European *Paliurus* Mill.

Some species, especially the two above, are widely cultivated as fruit trees. The wood of some is of local importance.

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7. **Reynosia** Grisebach, Catal. Pl. Cubens. 33. 1866; emend. Urban, Symb. Antill. 9: 225. 1924.

Evergreen shrubs or trees. Leaves usually opposite or subopposite [rarely partly alternate], coriaceous, entire, pinnately veined, with 6–15 pairs of inconspicuous primary veins and numerous finely reticulate veinlets visible only with magnification; stipules connate laterally at least half their length in the axil, persistent. Inflorescences axillary sessile, subumbellate, cymose fascicles, sometimes reduced to solitary flowers. Flowers small, yellowish green, 5-merous, perigynous, bisexual, pediceled. Floral tube short-campanulate to hemispherical; calyx lobes ovate, acute, spreading, deciduous. Petals wanting [or present]. Stamens shorter than calyx lobes, inserted on upper margin of disc; anthers elliptic in outline, dorsifixed near base, slightly versatile. Nectariferous disc fleshy, lining floral tube. Stigmata 2; style short, stout, 2-lobed; ovary superior, 2-locular, the 2 septa meeting in the center or overlapping each other and extending nearly to the opposite ovary wall, accumbent, but distinct; ovules pleurotropous. Fruit a small, subglobular to ellipsoid, purple to black, single-stoned drupe; mesocarp fleshy, thin; stone thickish, ± bony, ellipsoid-subglobular, usually 1-locular by reduction of the second locule, indehiscent. Seed ovoid to subglobular; seed coat membranaceous, thin, rugose, adherent to the endocarp; endosperm copious, hard, ruminate; embryo relatively small, the cotyledons oblong or elliptic, flat, the radicle elongate. LECTOTYPE SPECIES: *R. retusa* Griseb.; see N. L. Britton, N. Am. Trees 673. 1908. (Named after Alvaro Reynoso, 1830–1888, Cuban agriculturist and chemist.)

A West Indian genus of about 16 species. Subgenus NEOREYNOSIA Suesseng. includes nine species with petaliferous flowers, while subg. REYNOSIA includes seven, one in our area, all with apetalous flowers. *Reynosia septentrionalis* Urb., darling plum, red ironwood, a shrub or small tree of Cuba and the Bahamas, occurs in hammocks on the Florida Keys and in peninsular Florida ("north on east coast to central Florida," according to Little, U. S. Dep. Agr. Handb. 41: 361. 1953). Fruits of this species are edible and are said to be pleasantly flavored.

Despite its ruminate endosperm, the genus seems to be closely related to the West Indian *Krugiodendron* and *Doerpfeldia* Urb., on the one hand, and to *Berchemia* and its allies, on the other.

The close-grained, very hard and heavy wood of a few species (e.g., *R. septentrionalis*, *R. guama* Urb., *R. regia* Urb. & Ekm.) seems to be of some local importance.

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Under family references see HERZOG (pp. 154–158), SARGENT (pp. 720, 721), SUESSENGUTH (pp. 136–138), VIKHIREVA (1952, pp. 260, 261), URBAN, and WEST & ARNOLD (p. 138).

SARGENT, C. S. *Reynosia.* Silva N. Am. 2: 19–22. *pl. 56.* 1891.

8. **Krugiodendron** Urban, Symb. Antill. 3: 313. 1902.

Evergreen trees or shrubs. Leaves opposite or subopposite, thin and firm to coriaceous, entire, pinnately veined, with 4–6 pairs of slightly curved primary veins and coarsely reticulate veinlets ± prominent on the upper surface; petioles short, stout; stipules small, connate laterally at the very base in the axil, persistent. Inflorescences axillary, few-flowered, shortly peduncled to sessile, umbel-like cymes. Flowers 5-merous, small, greenish yellow, bisexual, pediceled. Floral tube broadly obconical, rather flat; calyx lobes triangular, acute, conspicuously crested on inner surface, erect or spreading, deciduous. Petals wanting. Stamens inserted under margin of disc, shorter than sepals, suberect in aestivation; anthers ovate to ovate-suborbicular in outline, obtuse. Nectariferous disc fleshy, broad-annular, ± 5-lobed, surrounding base of ovary. Stigmata 2, small; style short, stout, 2-lobed to -fid; ovary superior, 2-locular, the 2 septa overlapping each other, extending to the opposite ovary wall, accumbent, distinct; ovules pleurotropous. Fruit an ovoid to ovoid-subglobular, black, single-stoned drupe; mesocarp fleshy, thin; stone bony, 2-locular (one locule often ± reduced), 1(2)-seeded, indehiscent. Seed ellipsoid, ± compressed dorsiventrally; seed coat membranaceous, adherent to the endocarp; endosperm wanting; embryo large, the cotyledons elliptic to subobovate, plano-convex, the radicle minute, retracted between the cotyledons. TYPE SPECIES: *K. ferreum* (Vahl) Urb. (Named in honor of Leopold Krug, 1833–1898, German botanist, explorer of the West Indian flora.)

The single species, *Krugiodendron ferreum* (*Rhamnidium ferreum* (Vahl) Sarg.), black ironwood, of the West Indies and Central America (Guatemala to southern Mexico), occurs in hammocks on the Florida Keys and in peninsular Florida from Monroe and Dade counties north to Cape Canaveral (Cape Kennedy), Brevard County. The species is closely related to and perhaps congeneric with the monotypic Cuban genus *Doerpfeldia* Urb., which seems to differ from *Krugiodendron* mainly in the alternate leaves. The close-grained, hard wood is the heaviest occurring in the United States (specific gravity 1.3–1.4).

REFERENCES:

Under family references see HERZOG (pp. 153, 154), SARGENT (pp. 721, 722), and SUESSENGUTH (p. 147), and WEST & ARNOLD (p. 138).

SARGENT, C. S. *Rhamnidium*. Silva N. Am. 2: 27–30. *pl. 58*. 1891.

Tribe GOUANIEAE Reisseck

9. **Gouania** Jacquin, Select. Stirp. Am. Hist. 263. 1763.

Deciduous vines climbing by solitary tendrils located at apex of short sterile axillary shoots or laterally near the bases of inflorescences. Leaves alternate, membranaceous to subcoriaceous, pinnately veined, sometimes

± distinctly 3-nerved at base, with 4–7 pairs of ascendent curved primary veins, coarsely and ± remotely crenate-serrate, each tooth usually with a small patelliform gland. Inflorescences axillary and terminal spike- or raceme-like thyrses composed of glomerules. Flowers small, 5-merous, epigynous, bisexual [or more commonly bi- and unisexual], short pediceled to subsessile. Floral tube broadly obconical to subcampanulate; calyx lobes persistent. Petals whitish or greenish white, ovate, concave, short clawed, inserted under the margin of the disc in its sinuses. Nectariferous disc epigynous, fleshy, 5-lobed [or pentagonal]; each lobe (opposite a sepal) extended into a distinct short and rounded or apically bilobed [or elongated and acuminate] staminode-like structure. Stigmata 3, small; style 3-lobed to -furcate; ovary inferior, 3-locular; ovule pleurotropous. Fruit a 3-locular schizocarp with 3 rounded commissural wings [or rarely unwinged], splitting septicidally through each wing into three 2-winged indehiscent mericarps separating from a 6-parted carpophore. Seed obovate in outline, convex abaxially, somewhat angular adaxially, or lenticular; seed coat bony, shining; endosperm scarce; cotyledons roundish, plane, the radicle very short. LECTOTYPE SPECIES: *G. tomentosa* Jacq. = *G. polygama* (Jacq.) Urb.; see Britton & Millspaugh, Bahama Fl. 258. 1920. (Named after Antoine Gouan, 1733–1821, physician and botanist, author of the *Hortus Regius Monspeliensis*, 1762, and *Flora Monspeliensis*, 1765.)

A pantropical genus of nearly 50 species, about 20 in tropical America, extending north to Mexico, the West Indies, and Florida; an almost equal number in southeastern Asia, eastern Australia, New Caledonia, and Polynesia; and the remainder in Africa, Madagascar, and the Mascarene Islands.

*Gouania lupuloides* (L.) Urb., chewstick, with the range of the genus in America, occurs in hammocks on the Florida Keys and in southern peninsular Florida, north to Brevard and Manatee counties. In the West Indies, pieces of the stem are chewed to heal and harden the gums and to cleanse the teeth. The dried and powdered stems are used in making dentifrices.

The genus seems to be closely allied to *Reissekia* Endl. of Brazil, and to the East Indian-East African *Helinus* E. Mey. ex Endl. It also shows somewhat more remote relationships to *Ceanothus* and *Colubrina*.

REFERENCES:

Under family references see GEMOLL (pp. 412–420), PRICHARD (pp. 97, 98), SUESSENGUTH (pp. 166–171), TRELEASE (1897, p. 419), and VIKHIREVA (1952, pp. 280, 281).

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# A NEW DIOSPYROS FROM THE MISANTLA REGION IN MEXICO

ARTURO GÓMEZ POMPA *

THIS PAPER IS A CONTRIBUTION to a critical study of the flora and vegetation of the Misantla region in central Veracruz, México.

The region is bounded on the north by the Nautla river, on the south by the Sierra of Chiconquiaco (also called Sierra of Naolinco), on the east by the Gulf of México, and on the west by the road from Misantla to Martínez de la Torre.

This small region of about 1500 square kilometers ranges in altitude from sea level up to more than 2000 meters, has an annual rainfall of 1400 to 3000 millimeters, a rich superficial geology, and complex topography. These factors provide the ecological conditions for a rich flora and the varied vegetation types of the area. The region is also notable in being located near the northern limit of the warm, humid tropics in America. Many important tree genera of southern México, as, for example, *Terminalia*, *Vochysia*, *Bernoullia*, *Dialium*, and *Vatairea*, do not reach this area, and a few, such as *Aspidosperma*, *Dussia*, *Chione*, and *Pseudolmedia* apparently have their northern limit of distribution here. The ranges of many other genera, among them *Brosimum*, *Achras*, *Carpodiptera*, and *Zuelania*, extend farther north to San Luis Potosí and probably to southern Tamaulipas. On the other hand, some genera widespread in the eastern United States, such as *Liquidambar*, *Fagus*, *Magnolia*, and *Juglans*, are represented in the flora of the temperate, humid montane area in this region.

It is of interest that several outstanding collectors, including Schiede, Deppe, Liebmann, Karwinski, and Purpus have collected in the Misantla region. The type localities of many species and a few genera, among them such well known taxa as *Croton draco* Schlecht., *Quercus oleoides* Cham. & Schlecht., *Aspidosperma megalocarpon* Muell., and *Misanteca capitata* Cham. & Schlecht. (the name of this genus derived indirectly from that of the town of Misantla) are in or near this area.

One of the most interesting vegetation types in the area is a deciduous forest (*bosque caducifolio*) at an altitude of approximately 900 to 2000 meters above sea level, on ferrolithic acid soils rich in organic materials. The humidity is extremely high due to the frequent fogs. The original forest is rather well conserved because of the abrupt topography and the lack of roads. Among the most conspicuous tree species in the upper

* While working on a series of Mexican collections I am using the facilities of the Arnold Arboretum and the Gray Herbarium of Harvard University, as a fellow of the John Simon Guggenheim Memorial Foundation. I want to express my gratitude to these institutions and their officers.

canopy are *Liquidambar styraciflua*, *Quercus affinis*, and *Meliosma alba* reaching heights of more than 40 meters. Other notable tree species in this area are *Befaria glauca*, *Dendropanax arboreus*, *Oreopanax liebmanii*, *Podocarpus matudai*, *Symplocos coccinea*, *Ternstroemia sylvatica*, *Turpinia insignis*, *Magnolia schiedeana*, *Brunellia mexicana*, and *Weinmannia pinnata*. In the course of studying collections made in the Misantla area, I found a new persimmon from this deciduous forest. The description of the new species and a discussion of its relationship to other taxa of the genus are here presented.

**Diospyros riojae** Gómez Pompa, sp. nov.

Arbor 10–15 m. alta, foliis ellipticis vel oblongo-ellipticis, 4–12 cm. longis, 2–5.5 cm. latis, basi cuneatis breviter attenuatis, apice breviter acuminatis, acumine obtuso, lamina glabra supra et subtus nitida, costa supra impressa, nervis nervulisque numerosis supra et subtus prominentibus, graciliter elevatis. Flores ignoti. Fructus nitidus solitarius, subglobosus, pericarpio coriaceo-ligneo, endocarpio luteo, 4–4.5 cm. longo, 4–5 cm. lato; calyce fructifero 5-lobato, lobis oblongis, 1.5 cm. longis, 0.5–0.7 cm. latis.

Tree 10–15 m. high; branchlets glabrous or the young shoots sparsely tomentose. Leaves elliptic or oblong-elliptic, 4–12 cm. long by 2–5.5 cm. wide, glabrous, shiny on both surfaces, when dry olive-green on the upper surface and brown-green on the lower, subcoriaceous, pellucid-punctate, cuneate at base and slightly attenuate, the apex faintly arcuate, shortly acuminate, the acumen obtusish; midrib impressed above, prominent beneath, with 6–11 pairs of primary veins prominent on both surfaces, the marginal nerves conspicuous; petioles canaliculate above, 6 mm. long. Flowers unknown. Fruit subglobose, about 4–4.5 cm. high and 4–5 cm. broad, glabrous, shiny, green when fresh, light brown when dry (probably immature when collected); the exocarp coriaceous-ligneous, the endocarp fleshy, drying orange-yellow. Calyx deeply 5-lobed, lobes oblong, acutish, glabrous, 0.5–0.7 cm. wide, 1.5 cm. long; style probably 5-parted.

HOLOTYPE: Mexico, State of Veracruz, between Chiconquiaco and Misantla, in *Liquidambar-Quercus* forest, with *Magnolia*, *Meliosma*, *Juglans*, and *Turpinia*, 1350 m. alt., Aug. 13, 1962, *Arturo Gómez Pompa 789* (A). Isotypes, US and MEXU.

This species is named in honor of the late Dr. Enrique Rioja LoBianco, who contributed greatly to the development of biology in México and under whom I studied ecology and biogeography at the Universidad Nacional Autónoma de México.

Although only this single fruiting collection is known, *Diospyros riojae* is distinctive in the shape and size of its leaves, in the glabrous, shining leaf blades, conspicuously reticulate on both sides; and in the large globose fruit. There is variation in the shape of the leaves, some being asymmetrical, others symmetrical, and in the size which may vary on one branch, but

their shape is predominantly elliptic to oblong-elliptic. In Standley's *Trees and Shrubs of Mexico*, which includes the only relatively modern treatment available for the Mexican species of *Diospyros*, this new species will be identified as *D. conzattii* Standl. (*D. pergamentacea* Lundell) [1] but it may be easily distinguished by the following obvious characters:

| | DIOSPYROS RIOJAE | DIOSPYROS CONZATTII |
|---|---|---|
| LEAF SHAPE | Elliptic or oblong-elliptic. | Lanceolate or ovate-lanceolate. |
| LATERAL VEINS | Prominent on both surfaces of leaf. | Not prominent on either surface of the leaf. |
| VENULES | Reticulate on both upper and lower surfaces. | Not reticulate on the upper surface. |
| LEAF SURFACES | Shiny throughout. | Dull. |
| FRUIT SHAPE | Subglobose (4–5 cm. broad, 4–4.5 cm. high). | Depressed-globose (4 cm. broad, 2 cm. high). |
| EXOCARP | Coriaceous-ligneous (not wrinkling on drying). | Coriaceous (wrinkling on drying). |
| CALYX LOBES | Up to 1.5 cm. long. | Up to 2.7 cm. long. |

It seems unlikely that *Diospyros riojae* and *D. conzattii* are at all closely related, in spite of their superficial resemblance. In a search for other possible relationships, all of the materials in the collections of the Arnold Arboretum and Gray Herbarium, including representatives of nearly half of the perhaps 400 species in the genus, were surveyed. It was soon evident that a number of species from widely scattered areas share to varying degrees some of the distinctive vegetative characters of *D. riojae*.

In leaf characters, the combination of shiny, glabrous leaf blades, conspicuously reticulate on both surfaces is especially conspicuous in *Diospyros riojae*. Some 25 additional species show the same combination of characteristics, and about 27 more differ only in that the lower side of the blade was dull instead of shiny.

Even though the taxonomy of many of the species of the genus is in doubt and the identifications of many are not reliable, it seems worth while to enumerate the species which share with *D. riojae* the combination having the leaf blades glabrous, shiny and conspicuously reticulate on both surfaces:

**Mexico:** *Diospyros cuneata, D. anisandra.*
**West Indies:** *D. crassinervis, D. tetrasperma, D. caribaea, D. leonis.*
**Eastern Asia:** *D. metcalfii, D. susarticulata, D. sinensis, D. nitida.*
**India:** *D. choboënsis, D. crumenata, D. ebenum, D. fleuryana, D. mun.*
**Philippines:** *D. alata, D. curranii, D. pilosanthera, D. viridifolia.*

[1] Both *Diospyros conzattii*, described from Oaxaca, and *D. pergamentacea*, described from Chiapas, are known only from fruiting specimens. The two seem to be conspecific, the differences between them being minor and mostly in size. They are therefore combined here under the older name.

**New Caledonia:** *D. olen.*
**Polynesia:** *D. hillebrandii, D. ferrea* var. *subimpressa, D. samoënsis.*
**Australia:** *D. hebecarpa.*
**Africa:** *D. mespiliformis.*

It should be noted that there is a wide variation in these species in leaf shape, venation, and size (only species with leaves from 2–15 cm. long

FIG. 1. *Diospyros riojae* showing some details of leaf venation and calyx form (approximately 1 2 natural size). Drawn by Eileen K. Carroll.

were considered), but there is a striking resemblance between *Diospyros riojae* and two species from southeastern Asia (Hainan), *D. metcalfii* and *D. susarticulata*. These three species are similar, not only in the characters mentioned above, but in leaf shape, size, and petiole. On the other hand, they differ from each other in fruit and calyx characters.

In a taxonomically difficult genus such as *Diospyros* in which all of the species are dioecious and in which many are known only from fruiting materials, the possibility of utilizing vegetative characters is an intriguing one, and the general similarity of leaf characters of species from both eastern and western hemispheres offers a number of interesting suggestions:

1. The presence of this combination of leaf characters in such a large number of species leads one to think that these may be linked characters that cannot be explained as a random distribution of individual characters.

2. Apparently these characters do not have any significant value for adaptation to the environment, for the species in which they are found occur in a wide variety of ecological situations. The large number of species with this combination in Asia, India, and the Philippines may well be related to the great number of species of *Diospyros* in that area, while the scarcity of these characters in extratropical regions is probably related to the paucity of species. (Only 12 species of *Diospyros* occur in subtropical regions and only 4 are known from truly temperate climates (White, 1956).)

3. According to Hiern in his monograph (1873), the 25 species mentioned above fall into a number of different sections. However, these need to be reevaluated, especially in view of some of the characters used by him in distinguishing some sections, as, for example, "stamens quite glabrous" versus "stamens more or less hairy." One can certainly join White (1956) and Wood and Channell (1960) in saying that revision at the subgeneric level is needed. The data above suggest that leaves can provide some useful characters for this purpose. This suggestion is supported by Bakhuizen van den Brink (1936–1941) who used some leaf characters (prominent venation) as an aid in distinguishing sections in the subgenus DIOSPYROS (subgenus *Eudiospyros*) and by White (1956), who stated that "the leaves should contribute some useful secondary characters" for the revision of the subgeneric classification of the genus. However, so much remains to be learned of the importance of floral and fruiting characters that it is difficult to know just how to evaluate the vegetative characters. It is obvious, however, that these can be useful in the comparison of species (e.g., *D. riojae* vs. *D. conzattii*).

4. In spite of differences in calyx structure, and our lack of knowledge of the flowers, the vegetative resemblance between *Diospyros riojae*, *D. metcalfii*, and *D. susarticulata*, mentioned above, suggest that these three may furnish yet another example of relationships between the plants of the *Liquidambar* forests in Mexico with those of the eastern United States and eastern Asia (Sharp, 1951, 1959; Dressler, 1954; Li, 1957; Miranda, 1959). At present only *D. virginiana* (closely related to *D. lotus*, of

eastern Asia), occurs in the eastern United States, but among the fossil species there is one which matches strikingly the leaves of *Diospyros riojae*.

Some 23 species of *Diospyros* have been described from Cenozoic deposits in North America (LaMotte, 1952), but many of these, described only from leaves, may not represent this genus. MacGinitie (1941) says, "The leaves of *Diospyros* are easily confused with those of *Banisteria*, *Heteropteris*, *Chionanthus*, *Nyssa* and the leaflets of various legumes." To this list can be added several more Sapotaceae, Styracaceae, Moraceae, and Thymelaeaceae which could also be confused with some of the leaves of living and fossil *Diospyros*. Despite this, *Diospyros wilcoxiana* Berry (1916, *pl. 101, fig. 1*), described from the Lower Eocene of Tennessee is remarkably like the leaves of *D. riojae*. This species has also been reported from the Eocene of Texas (Ball, 1931); and it is worth mentioning that Ball also reported as *D. mirafloriana* Berry a deeply 5-parted calyx, similar to that of *D. riojae*. Thus it seems evident that many of the species of *Diospyros* with leaf characters similar to those of *D. riojae*, which today are restricted to tropical or subtropical regions (as are all of the species with a 5-lobed calyx), have come from a stock once much more widely distributed and continuous in the northern hemisphere. It is also remarkable that vegetative parts that at first sight look very variable can remain relatively unchanged through millions of years. The relationships of *Diospyros riojae* with other species of the genus remain obscure, but it is to be hoped that an eventual revision of the genus, including the fossil remains, will one day clarify these.

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# A FURTHER NOTE ON CEANOTHUS HERBACEUS VERSUS C. OVATUS[1]

GEORGE K. BRIZICKY

TORREY AND GRAY (Fl. N. Am. 1: 264–268. 1838) seem to have been the first to study critically the genus *Ceanothus* (Rhamnaceae) in the eastern United States. The large number of species described from that area up to that time (nearly 10 by Rafinesque, three by Pursh) was reduced by these authors to five, which have been recognized by all subsequent authors dealing with the flora of North America. Although Torrey and Gray's delimitation of these species was basically correct, some changes in the circumscription, or at least in the synonymy, of *C. americanus* L. and in the nomenclature of the species generally known as *C. ovatus* Desf. are necessary.

These two rather similar, but actually quite distinct, species are widely distributed in eastern North America, the first extending south to Florida, the second to central Tennessee and Arkansas in the southeastern United States. "When compared with each other these two species resemble each other very much from seedling to mature plant. But characteristic of *C. ovatus* is, however, the [short-peduncled] terminal inflorescences [in contrast with the axillary, long-peduncled inflorescences of *C. americanus*] and the narrower leaves with stomata on both sides" (T. Holm, Am. Jour. Sci. 22: 530. 1906). Although the leaves of *C. americanus* are typically ovate, rounded or subcordate at the base, and usually more or less pubescent, while those of *C. ovatus* are elliptical and typically glabrous, there are specimens intermediate between the two species in the shape of the leaves and the degrees of pubescence, as well. The further feature which is characteristic of *C. americanus* is that "the flowering branches [are] herbaceous, new each year" (Fernald, Gray's Man. Bot. ed. 8. 993. 1950), a character not recorded for *C. ovatus*.

Apparently this last character was the reason that *Ceanothus herbaceus* Raf., 1808, originally described as a plant with annual stems, was included in *C. americanus* by Torrey and Gray as var. *herbaceus* (Raf.) Torr. & Gray, with *C. perennis* Pursh in synonymy. Most botanists in the succeeding century generally followed Torrey and Gray in identifying *C. herbaceus* Raf. with *C. americanus*, rather than with *C. ovatus*. More recently, however, Shinners proposed (Field Lab. 19: 33, 34. 1951) to substitute *C. herbaceus* Raf., "1809," for *C. ovatus* Desf., 1809, on the basis of the presumed misapplication of the latter name. Although this proposal ap-

[1] Continuing a series of miscellaneous notes and papers on the flora of the southeastern United States made possible through the interest and support of George R. Cooley and a grant (GB-171) from the National Science Foundation.

parently has not met with general recognition, it induced me to investigate further the taxonomic and nomenclatural status of *C. herbaceus* Raf.

A few botanists prior to Shinners identified Rafinesque's species, described from "near the falls of the Potowmack, between the rocks," with that of Desfontaines, described from material cultivated in France. Thus, in 1919, Hitchcock and Standley (Fl. District Columbia, p. 201) noted under *C. ovatus*, "Plants from our region were described by Rafinesque as *C. herbaceus*." The authors of *The Flora of Vermont* (E. J. Dole, editor. ed. 3. p. 186. 1937) listed *C. herbaceus* in the synonymy of *C. ovatus*. Finally, Merrill (Index Raf. p. 162. 1949) referred *C. herbaceus* Raf., Med. Repos. II. 5: 360. 1808, to *C. ovatus* Desf., but quite inexplicably regarded *C. herbaceus* Raf., Jour. Bot. Desvaux 1: 227. 1809, as *C. americanus*, although Rafinesque's article in the *Journal de Botanique* was an exact translation of that in the *Medical Repository*.

Despite the discrepancies in the taxonomic treatment of Rafinesque's species, no attempts were made to reinvestigate its taxonomic and nomenclatural status until 1951, when Shinners proposed to substitute *C. herbaceus* Raf., 1809, for *C. ovatus* Desf., 1809. The conclusion he reached is correct, but the basis for the substitution is not. Having examined some recent collections of *Ceanothus* from the type locality of *C. herbaceus* Raf. and having compared the original description of the latter with that of *C. ovatus*, Shinners concluded that 1), although the type of Rafinesque's species was probably not preserved, his species is identifiable by the collections from the type locality; 2) *C. herbaceus* Raf., 1809, is conspecific with *C. ovatus* auct., not Desf., and with *C. ovalis* Bigel., 1824; 3) *C. ovatus* Desf. is an unidentified cultivated species (perhaps a hybrid), and "perhaps mere resemblance in name was an inducement to substitute *C. ovatus* for *C. ovalis*"; and hence, 4) *C. herbaceus* Raf., 1809, is to be substituted for *C. ovatus* Desf., 1809, the name of a different and unknown species.

The circumstance that in the vicinity of Washington, D. C., *Ceanothus ovatus* Desf. "is confined to the Potomac shore, where it inhabits the rocks at 'Little Falls'" (Holm, p. 523; see also L. F. Ward, Guide Fl. Wash., p. 72. 1881, and Hitchcock & Standley, *loc. cit.*), while *C. americanus* occurs in dry copses or in open fields (Holm, *loc. cit.*), fully supports Shinners' conclusion regarding the conspecificity of *C. herbaceus* with *C. ovatus*, but his statement that *C. ovatus* Desf. is an unknown species, different from that to which this name was applied, is incorrect.

In their treatment of *Ceanothus*, Torrey and Gray (Fl. N. Am. 1: 264, 265. 1838) at first placed *C. ovatus* Desf. in the synonymy of *C. americanus* [var.] γ. *herbaceus* (Raf.) Torr. & Gray, considering it different from *C. ovalis* Bigel. After having seen an authentic specimen of *C. ovatus* Desf., these authors (*loc. cit.*, p. 686) removed the latter from the synonymy of *C. americanus* var. *herbaceus* to *C. ovalis* Bigel. with the remark, "To this belongs *C. ovatus* Desf., which is the prior name, but less appropriate, as the leaves are never ovate." This authentic specimen of *C. ovatus* Desf., with the label "Herb. Webbianum. Ex Herb. Desfontaines," with

pencil marks on the sheet "W. T." [William Trelease] and "[type]," is preserved in the collections of the Gray Herbarium. Since *Ceanothus ovatus* Desf. is clearly typified in the sense in which the name has been used since Torrey and Gray, Shinners' second to fourth conclusions are untenable.

There is, however, another reason for taking up *Ceanothus herbaceus*: the priority of Rafinesque's name over that of Desfontaines. *Ceanothus herbaceus* Raf. was first published in 1808, not in 1809, thus antedating *C. ovatus* Desf., of 1809, and being the correct name for this species of northeastern and central North America.

**Ceanothus herbaceus** Raf. Med. Repos. N. Y. II. **5**: 360. 1808, "Canothus," sphalm.; Jour. Bot. Desvaux **1**: 227. 1809.

*C. ovatus* Desf. Hist. Arbr. Arbriss. **2**: 381. 1809.
*C. ovalis* Bigel. Fl. Boston. ed. 2. 92. 1824.

Topotype collections of *C. herbaceus* Raf. seen: In vicinis of Washington, D. C., *L. F. Ward*, July 18, 1880 [fruiting specimen] (GH). (The same sheet also bears a flowering specimen collected June 4, 1881.)

# THE DIRECTOR'S REPORT

## THE ARNOLD ARBORETUM DURING THE FISCAL YEAR ENDED JUNE 30, 1964

FROM THE POINT OF VIEW of active participation and representation in the many areas of its interest, the year just completed was a varied and successful one for the Arnold Arboretum. Several staff members made extended and intensive field trips which yielded botanical and horticultural collections, series of photographs, and impressions of value which will contribute significantly to their current and future work. The number and quality of published contributions by the staff continued at a high level. The Arboretum was represented at several professional meetings, and, in turn, welcomed many distinguished visitors.

At the open house scheduled for visitors on successive week-ends in May a moderate number came to Weston to the Case Estates. At Jamaica Plain, however, which is more easily accessible, the crowd was almost overwhelming in its enthusiastic pleasure with the flowering display.

**Staff:**

On January 1, Dr. Lily M. Perry retired officially from the staff of the Arnold Arboretum. Miss Perry, who joined the Arboretum staff in 1937, worked for a number of years closely with the late E. D. Merrill and was coauthor with him of a long series of papers on the flora of New Guinea. More recently, Dr. Perry has been compiling information on the medicinal plants of southeastern Asia. When this manuscript is published she plans to return to her major interest, work on the New Guinea flora, and will continue to be of assistance to the Arboretum staff on problems of the southeastern Asiatic area. Her long and devoted service has been of inestimable value to the institution and to all her colleagues.

During the year also, Mrs. Susan Delano McKelvey requested her retirement as a member of the Committee to Visit the Arnold Arboretum and as a Research Associate on the staff. Her services, which have been continuous since 1920, are deeply appreciated.

Dr. Lorin I. Nevling, Jr., was appointed Associate Curator and Supervisor of the Herbaria, jointly with the Gray Herbarium, to be in charge of the herbarium collections in Cambridge and in Jamaica Plain.

Dr. Shirley A. Graham, who had recently completed her doctoral studies at the University of Michigan, joined the staffs of the Arboretum and the Gray Herbarium in September to work for a year on the Southeastern Flora Project.

Mr. Andrey Baranov was appointed Curatorial Assistant. His special abilities with the flora of Manchuria will aid the staff in handling the accumulated collections from eastern Asia. The appointment of Dr. Mary E. Sanders as a Research Associate was renewed, as was the Mercer Fellowship awarded to Dr. Lalit Srivastava.

Dr. Howard was appointed to the Scientific Advisory Committee of the Fairchild Tropical Garden and to the Committee on Pioneering Research of the National Academy of Sciences — National Research Council.

Dr. Wyman was elected a Vice President of the International Dendrological Union and continued his services as a Director of the American Horticultural Society and as a Trustee of the Massachusetts Horticultural Society. At the International Shade Tree Conference held in Canada, the "Author's Citation" of that organization was awarded to Dr. Wyman "for sustained production of excellent books in the field of arboriculture."

**Horticulture:**

The climate of the past year was again unusual. The summer was dry with prolonged drought so that when the first rains came on October 1 there was a deficiency of ten inches in an expected normal rainfall, to that date, of 31 inches. During the winter, however, total precipitation became normal. Precipitation as snow, moreover, was the heaviest in 17 years, with a total of 63 inches. No severe storms were experienced, but an unusual one occurred on March 10 when sleet fell for eleven hours, accumulating to a depth of two inches before turning to snow.

The effect of these conditions on the grounds was not severe. The dry summer promoted the formation of many flower buds in the dogwoods, which produced an outstanding display in the spring. Some branch damage can be attributed to the summer dry spell, while during the winter, rabbit and mouse damage to trunks and stems of smaller shrubs was heavy under the deep snow cover.

A major improvement on the grounds is now under way. The construction of the first segment of a roadway to the top of Peters' Hill, mentioned in the report of the previous year, is a costly operation, and it was expected that completion might be delayed several years. The Department of Parks and Recreation, however, recognized the need for this road and turnaround, and, with its cooperation, continuation of the work during this fiscal year has been possible, with completion scheduled for this summer.

In the care of the living collections a particular effort was concentrated on the area near the Forest Hills gate. Dieback of the *Prunus* collection necessitated the removal of many of the older plants, which now have been replaced with dogwoods to allow a period of rest for the soil. Newer accessions of cherries or propagations from the older plants are being placed elsewhere on the grounds in an effort to limit the effect of virus and nematodes. Portions of the shrub collection have also been replanted. Experience has shown that this area near the Forest Hills gate collects cold air during the winter season and that many Leguminosae have been affected by the colder environment. These have been moved to other

"Winter Splendor." The result of a February snow storm in the Arnold Arboretum. Photo. courtesy of the Boston Globe.

locations, while a miscellany of shrubs is being planted experimentally to determine family or generic hardiness in that particular spot.

Because of the dry fall, planting was held to a minimum, but the early, cool spring offered an extended period for moving plants from the Case Estates to Jamaica Plain. A total of 558 plants, representing 250 taxa, was planted. Included in this number were 34 taxa of *Salix* for improvement of the collection in the meadow area.

It has been possible to continue use of cocoa shells for mulch, and approximately 566 tons were used during the year, with particular success under various tree collections. A "mulching material" being used around small-stemmed plants is sheeting of black polyethylene film, the effectiveness of which was described by Dr. Wyman in a recent issue of *Arnoldia*.

Faulty drainage caused by an underlying layer of compacted soil necessitated special work on two nursery beds in the area of the Dana Greenhouses. After the top soil was removed and a hardpan layer broken, drainage tile was installed and covered with ten inches of sand and gravel. An enriched top soil was replaced and left over the winter, apparently completely correcting the problem.

The regular activities of the greenhouse staff were carried on as usual, or increased in certain directions. During the past fiscal year the Arboretum received 153 shipments of whole plants of 731 taxa from 12 countries, including the United States, and 159 shipments of seeds of 485 taxa from 43 different countries. The increase in these figures this year reflects the travels of many staff members who sent back plant materials or requested additional materials seen on their travels for study or horticultural trial. On the other hand, the Arboretum sent in response to specific requests, or for its own research purposes, 159 shipments of plants of 969 taxa to 7 countries and 56 shipments of 172 taxa of seeds to 13 countries. Included in the shipments of living plants were specimens of selected taxa considered worthy of more extensive growth. Under the program for cooperating nurserymen the Arboretum distributed eight taxa to 57 nurseries and botanical gardens, or a total of 549 plants. One of these, *Hamamelis intermedia* 'Arnold Promise', represented a new selection developed on the Arboretum grounds and reported in detail in a recent issue of *Arnoldia*. Six of the remaining seven taxa were plants recently or originally introduced to the United States by the Arnold Arboretum. All have been tested for hardiness in Weston and have proven to be most desirable cultivated plants not otherwise available in the United States. Also, 266 taxa were propagated for eventual use on the grounds in Jamaica Plain or in Weston; and 186 taxa were propagated for the use of the staff.

Previously reported research projects of the greenhouse staff are continuing. Among the projects newly initiated during the year is a study concerned with the processing of seeds of second generation hybrids of *Rhododendron* proven hardy at a temperature of minus 45 degrees Fahrenheit. Seeds for this project were donated by Mr. Frank Abbott, of Saxons River, Vermont. Another new project concerned study of progeny from seed of abnormal growth forms, or witches' brooms, of pine and hemlock. Seed from cones of these abnormalities produce both normal and abnormal seedlings which are now being studied to determine whether the abnormalities are lost or whether they may become lethal.

At the annual meeting of the American Association of Botanical Gardens and Arboretums in St. Louis, the Arnold Arboretum was reappointed for the third time national registration authority for woody plants not already represented by designated individuals or societies. During the past year

one registration list was published, for *Fagus*; work continues toward the completion of lists for *Ulmus* and *Weigela* within the calendar year.

Dr. Dudley has continued his work on *Alyssum*, chiefly on floristic studies, but has initiated, also, hardiness trials of more than 40 species, in order to determine the full potential of this genus as a cultivated plant for New England.

Mr. Green has organized the collections made on his trip to the Pacific. The new collections and data on various Oleaceae are being studied. A few of the recent introductions of the family formerly under plant quarantine restrictions have been cleared and will be distributed to other areas for trial.

### Case Estates:

The interest in the plantings on the Case Estates in Weston continued to increase during the year. Past publicity and the maturity of some of the special collections have increased the educational value and the effectiveness of the displays. Additions were made to the trial plots of *Narcissus* and to the collection of *Lilium*. There are now more than 300 taxa of lilies, including one special gift of 52. In August, the New England section of the North American Lily Society made a special visit to the demonstration area. Additional beds have been prepared for display collections of *Hemerocallis*, *Iris*, and *Allium*, in the hope of developing a representation of the units of classification of each group, both for study by classes and for exhibition. The American Hemerocallis Society has offered material and financial support for work on those plants in which its members have special interest.

The perennial garden and the ground covers have had the majority of old labels replaced with engraved plastic labels.

Roads at 84–86 Wellesley Street were resurfaced in accordance with obligations to maintain access to this property, and one section was relocated for easier maintenance in winter snows.

A commercial survey of property lines along the Ash Street section was necessary following a petition by a neighboring property owner for construction at variance with town regulations. The boundaries of the Case Estates in this area, where 86 cultivars of *Chaenomeles* obtained in connection with the work of Dr. Weber have been planted, are now marked.

An open house was held on May 10.

### Herbarium:

The most conspicuous changes in the herbarium were made in the facilities for housing and studying cultivated plants in the Administration Building in Jamaica Plain. Forty-three new herbarium cases were purchased and installed on the second floor gallery, doubling the case capacity of the herbarium in the past three years. This entire section of the herbarium has been redecorated and new fluorescent lighting has been installed. The third floor gallery has also been thoroughly cleaned and painted, and the unmounted collections stored there have been re-examined

for study, mounting, and insertion in the general herbarium as soon as possible, in order to make them available to the scientific community. The entire horticultural herbarium has been redistributed in the cases now available, both to increase working space and to allow for more rapid insertion of specimens.

During the year 21,951 specimens were mounted and added to the herbarium collections in Jamaica Plain and Cambridge. The total number of sheets in the herbarium is now 785,660. During the year, 14,931 specimens were received, the greater portion by exchange. The areas represented in order of size were India, Papuasia, the West Indies, and Western Malaysia. A large collection was received from the Royal Botanic Garden in Edinburgh, comprising the collections of G. H. Cave from the mountainous areas of India. This is a particularly valuable addition to our Asiatic collections.

During the past year, staff members and students requested or received for identification 6,219 herbarium sheets representing 81 loans from 40 institutions, 23 in the New World, 17 in the Old World. The staff filled loan requests for 141 loans to 67 institutions (41 in the United States and 26 foreign), and sent out 14,617 specimens.

The taxonomists of the staff have continued and intensified their research studies, partly as a result of recent field work on special groups. Dr. George K. Brizicky, who has completed work on the Celastrales and Sapindales for the generic flora of the southeastern United States, has ready for publication a study of the genera of Rhamnaceae of the same region, and is now studying the genera of Vitaceae. Dr. T. R. Dudley is continuing studies of *Alyssum* and its relatives, of the family Cruciferae, particularly the representatives from Turkey and adjacent areas. Dr. Shirley A. Graham has completed treatments of the Lythraceae, Elaeagnaceae, Rhizophoraceae, and Combretaceae for the generic flora of the southeastern United States, and is continuing work on the Polygonaceae and Araliaceae for the same project, as well as studies on the genus *Cuphea*.

Mr. Peter Green's work has been augmented by his new Pacific collections of Oleaceae which will provide material basic for solving some of the numerous problems in that family. Dr. Howard is continuing taxonomic studies on various West Indian genera, toward completion of a flora of the region. Dr. Hu is continuing studies in the genus *Ilex* and on other problems in the Asiatic flora. Dr. Nevling is carrying on his studies in the Thymelaeaceae, a family in which many genera are poorly understood because of inadequate material. Dr. Schubert is continuing studies in the genera *Dioscorea*, *Desmodium*, and *Begonia*, material of which was collected in Mexico in the autumn. A collection of about 100 specimens of *Desmodium* was received during the year from the Department of Agronomy and Soil Science of the University of Hawaii, consisting of voucher material for chromosome counts of *Desmodium* species being grown in breeding programs for development of forage and for other uses.

Dr. Wood has continued his supervision and editing of the botanical studies and illustrations for the generic flora of the southeastern United

States for which he is also preparing treatments of Gentianaceae and Loganiaceae and a comprehensive glossary. Dr. Otto Solbrig, of the staff of the Gray Herbarium, contributed a treatment of the Tribes of Compositae for the Southeastern Flora Project, and Dr. Wallace Ernst, formerly attached to the same project, completed studies on the Berberidaceae, Lardizabalaceae, and Menispermaceae, which were published during the year.

Dr. Claude Weber, a former graduate student, whose work on *Chaenomeles* has already been mentioned, completed the taxonomic and morphological portions of her work which are in the process of publication.

**Library:**

The task of maintaining a highly specialized library so that current needs are met and gaps in older literature are filled, is a demanding one. Thanks to the acuity and energy of Mrs. Schwarten, however, our library continues in its superior position. Two of the interesting rare volumes added in the past year are the *Curioser Botanicus* of Samuel Mueller, published in Dresden and Leipzig, in 1730, a notable addition to the pre-Linnaean collection, and not known to be in any other library in the United States; and a first edition of John Lindley's *The Vegetable Kingdom*, which completes our series of this work.

Three hundred forty-five bound volumes, obtained by purchase, exchange, or as gifts were added to the library during the year. Of these, one hundred concerning horticultural subjects are housed in Jamaica Plain. The total number of bound volumes is now 52,217. Three hundred eighty pamphlets and reprints increased the total of that collection to 19,824. The 1500 cards of the 1963–64 issues of the *Index to American Botanical Literature* published by the Torrey Botanical Club, 3000 cards of the *Card Index of American Plants* issued by the Gray Herbarium, and sets 18 and 19 of the *Index Genericorum* were all added to existing files in Jamaica Plain and in Cambridge.

In a joint project with the library of the Gray Herbarium the microfiche reproductions of the historical botanical collections of various herbaria are purchased and housed in the library for maximum protection. During the year microfiche reproductions of the basic herbarium at the Botanical Museum and Herbarium at Copenhagen, Denmark, were made available, along with those of some of the special herbaria of that institution (among them the collections of Isert and Thonning, Vahl, Forskål and Rottböll). The microfiche reproductions have great value in taxonomic research, and continuation of this project will be most desirable.

We are always grateful for the donations of books, manuscripts, and biographical materials to the library, and acknowledge with pleasure the useful gifts during the year from Mrs. R. W. Bliss and Mrs. E. Corning.

**Comparative Morphology:**

In continuation of his studies on the comparative anatomy of the leaf-bearing Cactaceae, Professor I. W. Bailey has found, in the genus *Pereskia*,

that the characters of cuticle, epidermis, and stomata of leaves and young stems prior to periderm formation offer significant evidence for the differentiation of taxa in *Pereskia*, as well as for distinguishing *Pereskia* from other genera. In a study of the occurrence of crystals in the leaves of Cactaceae his studies indicate that two morphological and biochemical categories of crystals are present. Further detailed investigation is called for which may elucidate the evolutionary changes in metabolism essential for the survival of these plants in arid environments.

Dr. Lalit Srivastava completed a review article on the anatomy, chemistry, and physiology of bark which will be published in the *International Review of Forestry Research*. In addition, he has surveyed the distribution of lignin in the bark of numerous angiosperms and gymnosperms. This work will be extended to determine the site of lignin synthesis and the possible relationships of synthesis of lignin and other phenolic compounds. Dr. Srivastava is engaged also, in an electron microscope study of living cells in leaves and bark to determine the changes in cell protoplast during the period of frost hardiness.

Dr. Howard has expanded his examination of the nodal structure and the vascular anatomy of the petiole to additional plant families. The abundance of material accumulated during field work in Africa, Mauritius, Australia, and New Guinea has added 15 families and over 400 genera to the survey. A new nodal-petiolar pattern has been found in the Crassulaceae and a general occurrence of the type no. 4 nodal structure, accompanied by a unique vascular pattern, has been found in Zygophyllaceae.

During the year additions to the slide collection included many prepared from woods collected by Dr. A. C. Smith in the Fiji Islands. Slides of the Passifloraceae have been obtained in a program of exchange with the United States National Museum. A program of exchange of documented wood samples has begun with the Forest Products Research Institute, Laguna, The Philippines. A large number of samples of woods from Borneo was received from the Forestry Department in Sandakan.

## Cytology and Genetics:

Dr. Mary Sanders has completed a survey paper on artificial culture of embryos. She reports on her continuing work on the cytology and genetics of sorghum that a search is being made for cytological evidence to support the hypothesis, developed from genetic evidence, that colchicine-induced mutants result from chromosome changes. Chromosomes are being examined in the parent line, in six mutant lines, and in reciprocal $F_1$ hybrids between parent and each mutant line. An investigation of colchicine treatment of four tetraploid sorghum lines, and of their corresponding diploid lines, also is in progress, in which diploid mutants have been obtained from both tetraploid and diploid seedlings.

Mrs. L. Rudenberg, Research Associate of the Gray Herbarium, has developed an interest in verifying cytological counts for plants in the living collections of the Arnold Arboretum. Regrettably, much of the early work published on chromosome counts of cultivated plants in the Arbo-

retum was not documented. Mrs. Rudenberg's present work involves plants under taxonomic study, such as *Psychotria*, or those soon to be studied. Chromosome numbers and cytological peculiarities are noted, with annotations made on herbarium vouchers and on the master locator cards in the Arboretum files.

A portion of Dr. Nevling's investigations of *Daphnopsis* species is also devoted to cytological studies which, up to now, have been inadequate for many representatives of this family. During the past year the first counts were published for species of *Daphnopsis* obtained as part of the field program in Puerto Rico last year.

Education:

No formal courses were offered by the Arboretum staff members during the year, but Messrs. Green, Howard, and Wood took part in presenting Biology 247, a course in plant geography. Graduate, undergraduate, and special students were assigned to staff members during the year for supervision of special research projects. These involved such diverse investigations as a review of the species of *Hopea* in the Philippine Islands, preparation of a check list of the cultivated plants of St. Croix, and study of the origin of homostylous pollen-trimorphic plants of *Psychotria guadalupensis*.

The informal Fall and Spring Field courses conducted by Dr. Wyman, Dr. Dudley, and Mr. Green in Jamaica Plain and Weston were well attended. Mr. Fordham again conducted a course in plant propagation using the facilities of the greenhouses. Dr. Howard, assisted by Dr. Wood, conducted a course in economic botany which considered the food plants offered by restaurants in the Boston area, for a selected group of dieticians. The full staff participated in taxonomic seminars held in the Harvard University Herbarium in Cambridge.

Staff members attended scientific meetings associated with their special research interests. Dr. Howard and Mr. Fordham presented papers during the regional meetings of the American Society of Horticultural Sciences held in Cambridge. Mr. Fordham was a speaker at the annual meeting of the Tennessee Nurserymen's Association, at the meetings of the International Plant Propagators Society in St. Louis, Missouri, and for the short course of the Connecticut Nurserymen at Storrs, Connecticut. Dr. Wyman was the speaker at the Awards Banquet of the American Horticultural Society in St. Louis, and at the annual meeting of the Garden Club Federation of Massachusetts. Dr. Howard gave the Laura L. Barnes lecture for the Morris Arboretum in Philadelphia, spoke in the lecture series of the Royal Canadian Academy in Toronto, and to the New York Horticultural Society. During his Australian trip he was invited to speak to the western section of the Australian and New Zealand Association for the Advancement of Science, in Perth. Messrs. Dudley, Green, and Howard were all speakers for the Boston Horticultural Club.

Dr. Schubert served as chairman of a section of contributed papers and presented a paper on *Desmodium* at the Second Mexican Botanical Congress.

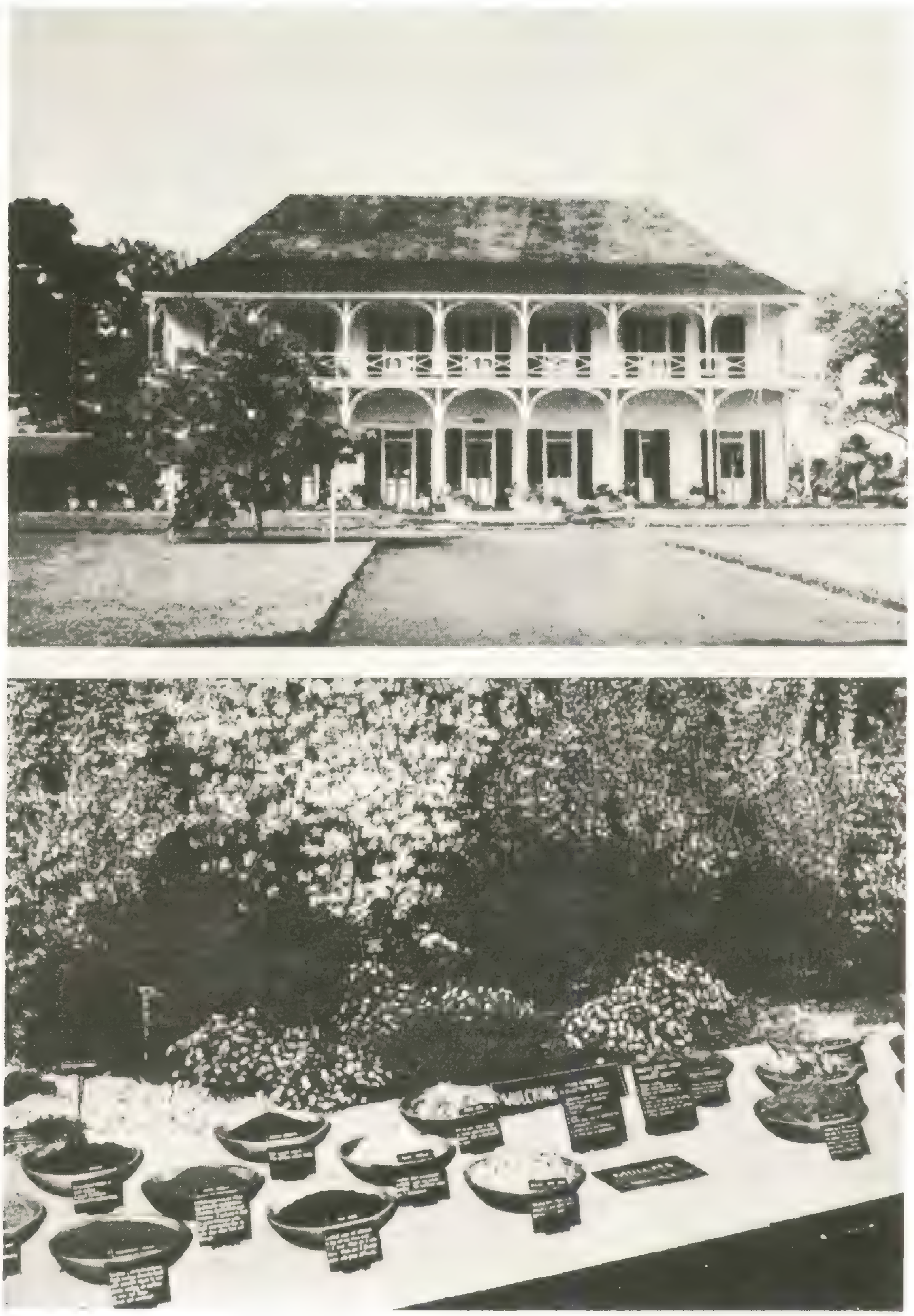
An exhibit of the Arnold Arboretum, in cooperation with the Horticultural Committee of the Garden Club of America, at the International Flower Show in New York. Photo. by J. Hugelmeyer.

Dr. Wood was invited to speak on modern distributional patterns in seed plants in a symposium on "The Origin and Evolution of the Biota of the Southeastern United States," during the annual meeting of the Society for the Study of Evolution held at the University of North Carolina, Chapel Hill, North Carolina.

These, and many other talks given by members of the staff, at the Arboretum or in other locations, form an important part of the educational contribution of the Arnold Arboretum. The preparation of mimeographed leaflets for distribution by the Garden Club of America represents another aspect of the educational program.

**Exhibits and Displays:**

Two large exhibits were prepared by the staff during the year. An exhibit on the propagation of woody plants by seeds was prepared at the request of the Horticultural Committee of the Garden Club of America for the International Flower Show in New York. This was similar to the exhibit last year at the Boston Flower Show, and was awarded the Director's Trophy. The staff prepared for the Boston Spring Flower Show of the Massachusetts Horticultural Society, in Boston, "an exhibition of mulching materials." A garden using different kinds of mulching materials formed the background for a display of wooden bowls containing samples



TOP: Administration building of the Royal Botanical Garden, Pamplemousses, Mauritius. A garden visited by Dr. Howard for its importance in the transfer of economic plants from the East Indies to the West Indies.

BOTTOM: The exhibit of mulching materials presented by the Arnold Arboretum at the Spring Flower Show of the Massachusetts Horticultural Society, 1964.

of the materials at close range for visitors' viewing. This exhibit was awarded a gold medal and an educational certificate.

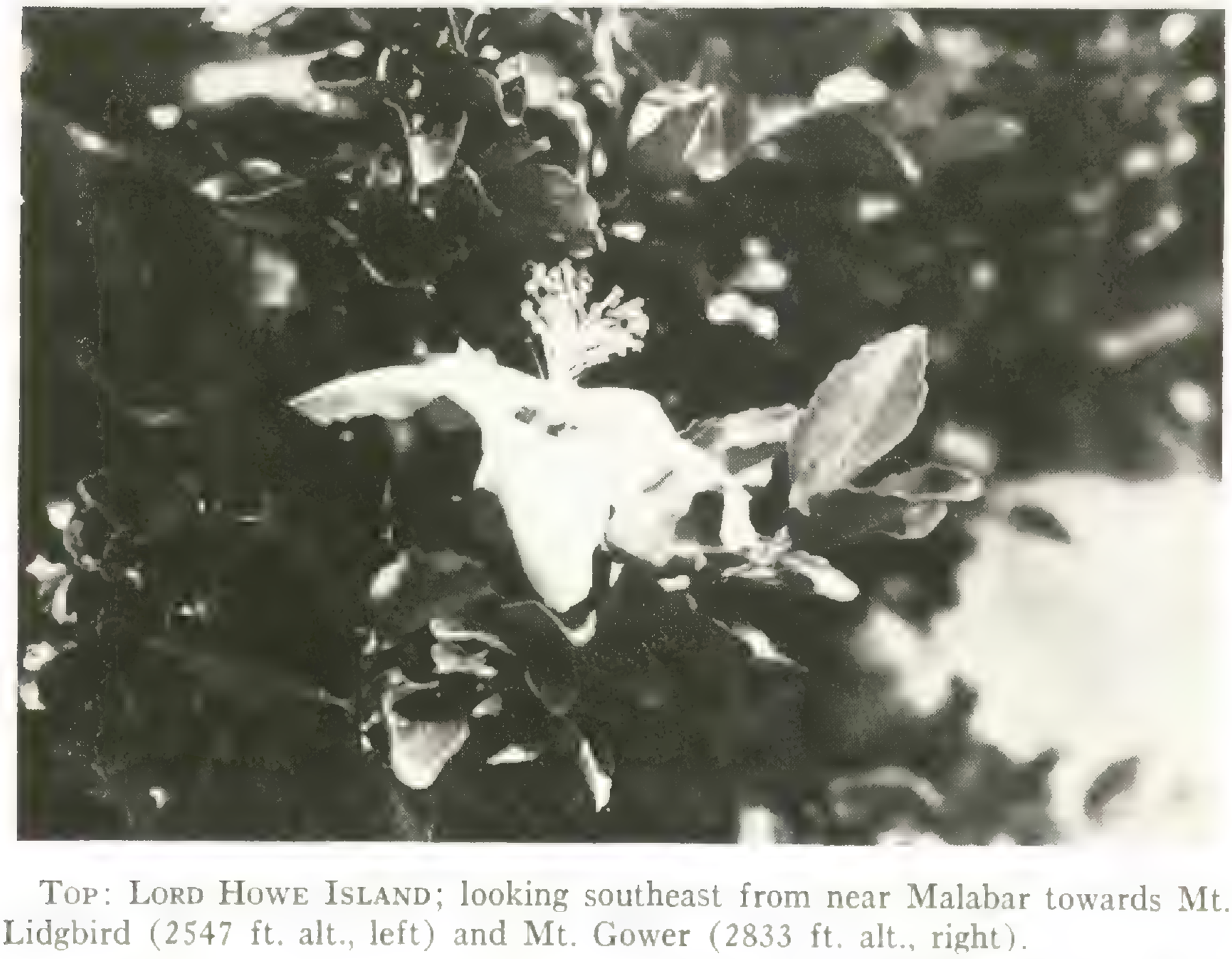
**Travel and Exploration:**

The opportunity to observe, collect, and study plants in the field and under cultivation is both a privilege and a requirement for the botanist. During the past year staff members of the Arboretum worked close to the Arboretum and in distant countries. From their efforts have come specimens dried as herbarium material, preserved for anatomical or cytological studies, photographed for teaching and lecturing, as well as living material for growing in greenhouse or out-of-doors for scientific study and for horticultural application.

Dr. Dudley undertook the task of adding to the representation of cultivated plants in the herbarium. We appreciate the kindness of owners of private gardens who gave permission for the preparation of herbarium specimens from their cultivated plants in localities at Mt. Desert Island, Maine, Chatham, Cape Cod, Massachusetts, near Albany, New York, and Philadelphia, Pennsylvania. Specimens of representative holly cultivars were also made available after the meeting of the Holly Society of America at the Callaway Gardens, Georgia.

Mr. Green, with the partial support of a grant from the National Science Foundation, made a trip to the Pacific to study plants of the Oleaceae and to make general collections in a few areas. His itinerary included the Hawaiian Islands, northern and western Fiji, New Caledonia, the north island of New Zealand, Norfolk Island, New South Wales, Victoria and Western Australia, and Lord Howe Islands. His collections from Norfolk and Lord Howe Islands were nearly all new to American herbaria and those of New Caledonia only slightly less so. Collections of certain families were made for specialists; and cuttings and seeds of Oleaceae and special groups for further study, or for possible horticultural introduction, were sent to the Arnold Arboretum, Foster Garden in Honolulu, the University of California Botanic Garden at Berkeley, the Los Angeles State & County Arboretum, Melbourne Botanic Garden, and the Royal Botanic Gardens at Kew and Edinburgh. Cytological collections made for Dr. Barbara Briggs of Sydney have yielded chromosome counts for 12 species in five genera of the Oleaceae not previously reported and a count for the puzzling genus *Oceanopapaver*. Dr. Otto Solbrig obtained clear counts from *Sciaphila* buds from New Caledonia, in a family which is scarcely known cytologically.

Dr. Howard spent two and a half months in the autumn on a trip around the world. He attended the plenary sessions of the AETFAT (a society devoted to the study of African botany) in Genoa, and then with most helpful assistance of botanists in many areas, was able to visit gardens and herbaria in Egypt, Ethiopia, Kenya, Mauritius, many parts of Australia, New Guinea, and Fiji. The initiative for the trip was an invitation to take part in a botanical tour commemorating the 50th anniversary of the founding of the Kirstenbosch Botanical Garden and the Natural History



TOP: LORD HOWE ISLAND; looking southeast from near Malabar towards Mt. Lidgbird (2547 ft. alt., left) and Mt. Gower (2833 ft. alt., right).

BOTTOM: HIBISCUS INSULARIS Endl. on Philip's Island (near Norfolk Island) where it is endemic, and of which only four bushes remain. Seed and cuttings were obtained.

Society of South Africa. After meetings in Capetown and local tours to places of botanical interest, the group of 41 visiting botanists representing 21 countries was taken on a 5,000 mile, 30-day tour of South Africa. As a botanical and horticultural introduction to the local vegetation and to the many introduced plants the tour could not have been better planned. Dr. Howard photographed many plant families and genera not usually available for use in classes, and also collected seeds, cuttings, and morphological material for further study.

Visiting botanists at the Kirstenbosch Golden Jubilee, September-October, 1963.

In April Dr. Howard, with Mr. Draper made a short trip to Puerto Rico to establish a small test garden for research purposes on land offered to the Arnold Arboretum on the south side of the Luquillo Mountain range.

Dr. Hu studied *Ilex* collections at the National Arboretum in Washington, and in several nurseries in Maryland. She also examined collections of the Meserve Arboretum on Long Island, in May, and obtained materials of hybrid plants for the horticultural herbarium.

Dr. Nevling represented the Arnold Arboretum at the dedication of the new herbarium facilities at Michigan State University in East Lansing. At a symposium held then, concerned with the role of "The Herbarium in the Modern University," curators from many institutions had the opportunity for discussion of professional problems.

Some botanists on Mt. Richmond, Victoria, Australia. Left to right: Clifford Beauglehole, Dr. Richard T. M. Pescott, Dr. James Willis, Fred Davies, Noel Learmont. Photo. by R. A. Howard, guest of this field party.

Dr. Schubert spent five weeks after the Mexican Botanical Congress collecting in the states of San Luis Potosi, Jalisco, and Nayarit, Mexico, and a week studying in the herbarium of the National University of Mexico in Mexico City. The cooperation of the botanists of the Botanical Garden of the National University and of the Forestry Department of the Mexican Government greatly expedited her work.

**Gifts and Grants:**

The Arboretum has gifts of many kinds in support of its work. The help of the Friends of the Arnold Arboretum which has been most generous is gratefully acknowledged. Herbarium specimens of particular interest were received from the Department of Agriculture in Bermuda and from the agricultural station of St. Croix. Books and back numbers of journals have been useful in filling some gaps in the library and in making available useful second copies for the use of the staff.

Various nurseries have made gifts of cultivated plants not represented in our living collections. The American Hemerocallis Society is supplying cultivars of daylilies for a collection in Weston, along with the funds for their maintenance. Mrs. F. W. Warburton of the Median Iris Society is contributing a collection of iris taxa for display. The Jan de Graf Company is helping to complete the representation of lily taxa in the collection in Weston.

Grants from the National Science Foundation helped to support the field

II Mexican Botanical Congress, San Luis Potosi, Mexico, September, 1963.

work of Mr. Peter Green in the southwest Pacific; support the investigations of Professor Bailey, and contribute to the support of the Southeastern Flora Project conducted by Dr. C. E. Wood. Grants for travel to the X International Botanical Congress were received by Dr. S. Y. Hu and Mr. P. Green.

**Publications:**

Under the editorship of Dr. Bernice G. Schubert four issues of the *Journal of the Arnold Arboretum* (now in its 45th volume) were published during the fiscal year, containing 515 pages and 23 articles, 21 of which were by members of the staff or former students. Dr. Wyman served as editor of *Arnoldia* (in its 24th volume) which appears at irregular intervals. Sixty pages were issued during the year.

In commemoration of the founding of the oldest botanical garden in the West Indies, on the island of St. Vincent, in 1765, the Arnold Arboretum is issuing a photocopy reproduction of the Rev. Lansdown Guilding's catalogue of the garden, originally published in 1825. Copies of the reproduction will be made available for the celebration on St. Vincent, and to libraries as well.

Another special publication is a photocopy reproduction of Dr. Donald Wyman's *How to Form an Arboretum*, of which a revised version was published as a number of *Arnoldia* in 1960.

The bibliography which follows lists 67 articles and books by members of the staff which were published during the past fiscal year.

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RICHARD A. HOWARD, *Director*

## Staff of the Arnold Arboretum

### 1963–1964

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IRVING WIDMER BAILEY, S.D., Professor of Plant Anatomy, *Emeritus*.
KARL SAX, S.D., Professor of Botany, *Emeritus*.

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CARROLL EMORY WOOD, JR., Ph.D., Associate Curator.
DONALD WYMAN, Ph.D., Horticulturist.

* Appointed jointly with the Gray Herbarium.
** Resigned 1964.
*** Retired 1 January 1964.

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